

Some Considerations of Population Dynamics and Economics in Relation to the Management of the Commercial Marine Fisheries¹

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INTRODUCTION

FISHING is one of man's oldest occupations; some of the sea fisheries pre-date recorded history. So long, however, as men relied on oar and sail to reach the fishing grounds, and on simple, hand-operated gear to catch the fish, the intensity of fishing on the high seas remained low, so that the amount of the catch had apparently little effect on the magnitude of the fish stocks. There were great variations in the harvests, of course, but these were due to fluctuations in the fish populations quite independent of the amount of fishing. A fisherman's success depended on uncontrollable natural factors, and was not much affected by whether the number of fishermen was many or few.

With the industrialization of sea fishing in the latter part of the last century, bringing steam and later diesel power to the vessels, and bringing new and more efficient types of fishing gear, and machinery to handle it, the sea fisheries near northern Europe and in some other parts of the world began to show signs of diminishing return per unit of fishing effort. Near the turn of the century, there was considerable controversy as to whether or not the amount of a given kind of fish which man is able to take from the sea is sufficient to have any noticeable effect on the supply. This matter was discussed at some length, for example, by McIntosh (1899), Garstang (1900) and others. Alfred Marshall was preparing the first edition of his famous *Principles of Economics* (1890) at the time when the industrialization of the British trawl fishery was proceeding rapidly and this controversy was going on. It was, therefore, yet a moot question whether his Law of Diminishing Returns applied to the sea fisheries (Marshall, 8th edition, 1938, p. 166).

Subsequent history of the North Sea demersal species, the haddock of Iceland and the Northwest Atlantic, the Pacific halibut, and of numerous other fisheries, leaves little room to doubt that a modern commercial fishery can so affect the stock of fish in the sea that the return per unit of fishing effort is thereby diminished, and can even become so intense that the *total* harvest is also reduced. It may be noted here, although the matter will be developed in more detail later, that the law of diminishing returns as applied by Marshall and others to agriculture is somewhat different than the application to the sea fisheries. As originally developed, the law holds that the increased application of other factors of

¹Received for publication January 14, 1957.

production to the land results in a decreased *rate* of return, but so long as the fundamental fertility of the land is not reduced, the *total* return would not diminish, but would increase, at a falling rate, toward some upper limit determined by the fertility of the land, the rainfall, amount of solar radiation, etc. (Ricardo's "original and indestructible powers of the soil".)

Experience having shown that the stock of commercial sizes of a sea-fish species, and the annual harvest obtainable from that stock, is related to the amount of fishing effort applied, there arises the important question of how the amount of fishing should be managed in order to provide the greatest benefits to mankind. This, of course, is a socio-economic problem which will have unique solutions only if it can be specified what situation among possible alternatives is to be regarded as most beneficial. Fundamental to rational consideration of the matter, however, is knowledge respecting what are the possibilities, which must depend on the dynamic relationships between amount of fishing and amount and yield of the fish stocks, and corollary economic implications.

Attempts to systematize some of the significant biological and economic facts bearing on this problem have been made by a number of persons in recent years, among which may be cited Russel (1931), Graham (1935, 1939, 1953), Beverton (1953), Gordon (1953, 1954), Burkenroad (1951), and Schaefer (1954a, b). The main result has been a considerable advance in our understanding of the biological and economic principles involved. There is, however, a fairly large degree of confusion, resulting from the biologists' inadequate consideration of economic principles, and, in part, from economists' failure to fully consider the properties of a self-renewing natural resource, the rate of renewal of which is dependent on the magnitude of the stock of the resource, which importantly distinguish such a resource from other classes of natural resources.

It seems worthwhile, therefore, to consider together some significant aspects both of the population dynamics of commercial fish stocks and of the economics of commercial fishing in order to arrive at a rational basis of considering the social problem of fisheries management.

In considering the bionomic properties of a fishery we shall be concerned with the "long run" relationships. That is, we are interested in the average annual harvests that will be *sustained* by the fish population indefinitely at different levels of fishing effort, the monetary value of the harvests, and the monetary cost of the fishing effort. This approach has been admirably and carefully applied by Gordon (1954), but some further consideration appears to be necessary, because (1) he has not made the necessary distinction between the self-regulating, density dependent fish resources and other common-property resources of a different nature, (2) the mathematical model in Section IV of his paper is not consistent with the assumptions in Section III (and is not quite in accord with some dynamic properties of fish populations), and (3) he has (p. 129) defined the optimum degree of utilization of any particular fish stock as that which maximizes the net economic yield, the difference between total cost, on the one hand, and total receipts (or total value production), on the other. This is one possible choice, of course, but it is not immediately obvious that it is the social optimum;

indeed other possibilities have been explicitly chosen both for particular fisheries² and as a general objective of fishery management.³

DYNAMICS OF RENEWABLE NATURAL RESOURCES

The natural resources upon which mankind depends are of two classes. In one class are those resources, such, for example, as fossil fuels, mineral deposits, and elements capable of yielding energy by the conversion of mass to energy by nuclear processes, which are non-renewable, or for which the rate of renewal is so slow that it is infinitesimal compared to the rate of use. To this class of resources the concept of indefinitely sustainable yield cannot be applied. Man can use these resources rapidly or slowly, efficiently or inefficiently, but the total quantity on this planet is limited and is subject to being completely used up in finite time. In the second category are those resources which are constantly renewed, and are, therefore, capable of yielding sustained production indefinitely.

The different nature of renewable and non-renewable resources was clearly distinguished by Marshall (p. 166-167). Among the renewable resources there are, again, two types with fundamental difference, those for which the rate of renewal is dependent on the amount of the resources which is left unharvested to perpetuate itself, and those where such dependence does not exist, or is negligible.

NON-SELF-REGULATING RESOURCES

For the second type, noted in the preceding paragraph, which we may call *non-self-regulating resources*, the amount which is available to be used each year is determined by natural phenomena other than the magnitude of the resource itself, and the amount which is used during a given year has no effect on the amount which will be available for use during the next year. The renewal of resources of this type is, consequently, independent of the rate of use.

The concept of "land" as one of the factors of production in classical economic science is apparently based on the idealization of this type of resource. The concept is summarized by Marshall (p. 144):

"While man has no power of creating matter, he creates utilities by putting things into a useful form; and the utilities made by him can be increased in supply if there is an increased demand for them: they have a supply price. But there are other utilities over the supply of which he has no control; *they are given as a fixed quantity by nature* and have therefore no supply price. The term "land" has been extended by economists so as to include the permanent sources of these utilities; whether they are found in land, as the term is commonly used, or in the seas and rivers, in sunshine and rain, in winds and waterfalls."

²The Convention between Canada and the United States of America for the Preservation of the Halibut Fishery of the Northern Pacific Ocean and Bering Sea, for example, provided for regulations "designed to develop the stocks of halibut in the Convention waters to those levels which will permit maximum sustained yield".

³The International Technical Conference on the Conservation of the Living Resources of the Sea, 16 April to 10 May, 1955 (Rome), attended by representatives of 45 nations, decided "The principal objective of conservation of the living resources of the seas is to obtain the optimum sustainable yield so as to secure a maximum supply of food and other marine products".

One example of this type of resource is hydro power. The amount of power which can be obtained annually from a river system depends on the rainfall, the topography of the land, and certain other physical factors (Massé and Rousselier, 1951). The amount which is used is always less than the amount potentially available, because of economic factors, but the amount used in a year has no effect, in general, on the amount which can be obtained in subsequent years.

A more familiar example, which has been the basis of much classical economic theory, is the use of agricultural land to produce cultivated crops from planted seed. As we have noted above, the land is considered to be a fixed factor of production, the amount of which can neither be increased nor diminished by man's actions. Since the quantity of this factor is fixed, the application of increasingly large quantities of other factors of production (labour and capital) to the land results in a decreasing return per unit of these other factors. So long as the inherent natural properties of the land are not destroyed, increasing effort will give increasing return, but the return per "dose" of capital and labour decreases. In other terms, production as a function of effort (number of "doses" of capital and labour) is a monotonically increasing function with negative second derivative, approaching some upper limiting value asymptotically. This may be illustrated by Fig. 1.

It should be noted that, for this type of resources, there is no maximum in the production function, since $\frac{dL}{dE} > 0$ for all finite E . In this respect such resources differ importantly from the self-regulating resources, the supply of which is influenced by man's action.

SELF-REGULATING RESOURCES

Populations of sea fish belong to a different type of natural resources, for which the annual rate of renewal of the resource is a function both of the physical environment, which is presumably constant, on the average, over the long run, and of the magnitude of the standing crop, or population, of the resource, which is diminished by the rate of harvesting. Some other populations of organisms are also of this same type, such as populations of wild, fur-bearing animals, forests which depend on self-seeding for renewal, herds of range cattle, range grasses (forage), and insect populations. In this last instance, man is usually interested in minimizing the population rather than in obtaining a high yield, but the same basic principles of population dynamics are involved. I shall, in the following, discuss primarily sea-fish populations, but the analogies for other similar resources should be obvious.

An outstanding common characteristic of populations of fishes, and other natural populations of organisms, is that they tend to remain in dynamic balance, neither falling to zero nor increasing without limit. Over any reasonably long period of time, losses from the population must be balanced by accessions to the population. When, however, the percentage rate of loss is increased, decreasing the size of the population, from whatever cause, the percentage rate of renewal must increase also, so that the population again comes into balance. This has been demonstrated in some detail by a number of biologists, from both theoretical

and experimental viewpoints, including Nicholson (1954,a,b), Ricker (1954), Lack (1954), and others. From the standpoint of the fish population, the harvesting by man is simply an additional source of mortality by predation, which is met by a compensatory increase in the rate of population renewal, so that the population again comes into balance at some lower population level at which the increased rate of growth of the population balances the harvest taken by man. For each size of population, there is a certain *rate of natural increase*, which is, under average environmental conditions, some single valued function of population size. In mathematical notation

$$\frac{dP}{dt} = f(P) \quad (1)$$

The catch, or landings, L , during a year is some function of the size of population and the amount of the other factors of production, which we collectively term "fishing effort", E .

$$L = \phi(P, E) \quad (2)$$

In the equilibrium state, which we are here discussing, the catch is exactly equal to the rate of natural increase. This has been called the *equilibrium catch* by Schaefer (1954a). This equilibrium catch is the long-term annual production of the fishery for a given level of population (and effort).

It immediately follows, of course, from (1) and (2) that under equilibrium conditions population size is some function of fishing effort

$$P = \Psi(E) \quad (3)$$

Data from experimental animal populations and from the commercial fisheries (Büchmann 1938, Graham 1935, 1939, Schaefer 1954a) indicate that $f(P)$ is a single valued positive function, falling to zero at $P=0$ and at $P=M$, the maximum population which the environment will support under average conditions, with no fishing, and having a maximum at some intermediate value of P . It further appears that a reasonably good first approximation is the quadratic

$$f(P) = k_1 P(M-P) \quad (4)$$

where k_1 and M are constants.

It also appears that, to a good degree of approximation,

$$L = k_2 EP \quad (5)$$

where k_2 is a constant so that, under equilibrium conditions,

$$k_2 EP = k_1 P(M-P) \quad (6)$$

and, consequently

$$P = M - \frac{k_2}{k_1} E \quad (7)$$

That is, for equilibrium conditions population size is a linear function of fishing effort; and, from (5) and (7)

$$L = k_2 E \left(M - \frac{k_2}{k_1} E \right) \quad (8)$$

It is to be noted that this mathematical model is identical with that derived by Gordon (1954) in section III of his paper and illustrated in his Fig. 1. It does *not* correspond to the model in section IV of his paper, where he assumed the population size to be a linear function of equilibrium catch, which is not in agreement with his earlier model, and is not in accordance with the experimental

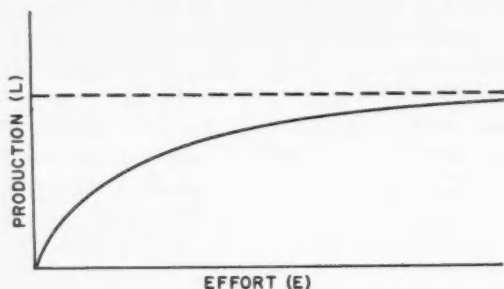


FIG. 1.

and observational data, because a necessary consequence of his last model is that equilibrium catch increases continually with fishing effort, having no maximum value at some intermediate level of fishing effort.

The production function, in terms of total weight of catch, of a fishery is the equation (8), shown graphically in Fig. 2.

For some fisheries, where the fish below the minimum commercial size constitute an important part of the breeding stock, the production may not fall to zero with increasing effort applied to the commercial stock, but will asymptotically approach some limiting value of production greater than zero, as shown, for example, by Beverton, *op. cit.* Over the range of values of effort which will be encountered in practice in such fisheries, however, my equation (8) still seems to provide a fairly good approximation.

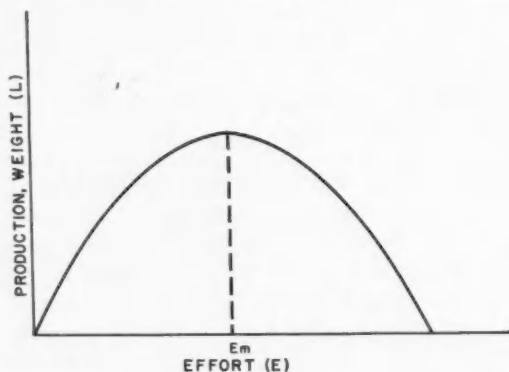


FIG. 2.

If the price of fish remains constant, i.e. if the demand is perfectly elastic, this is also the production function in terms of value. If, however, there is some decrease of unit prices with quantity marketed, the production function in terms of value, V , will have a somewhat different form.

The form of V as a function of E will depend on the demand-price function, but it is to be noted that so long as the price elasticity of demand remains greater than unity, the production function in terms of value will have its maximum at the same level of effort as the production function in terms of quantity (Fig. 3, Curve A). If the elasticity of demand becomes less than unity for some levels of production which the fishery is able to reach, there may be two maxima in the production function in terms of value (Fig. 3, Curve B). The zero points of the two functions will be identical under any circumstances, because zero catch is of zero value whatever the unit price.

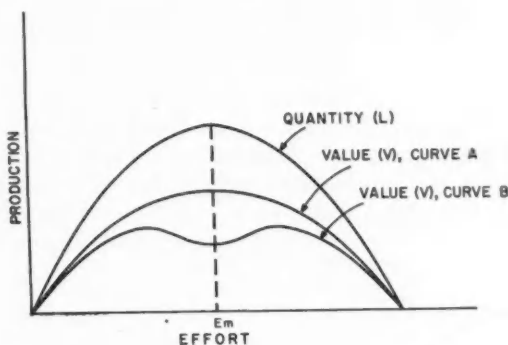


FIG. 3.

For most individual stocks of sea fish, the catch is a rather small share of the total production of all fish with which it competes in the market, and, therefore, it seems reasonable to assume that for the products of a particular fish stock the elasticity of demand is large. Indeed, we should not go far wrong in assuming, as has Gordon (1954), that the price does not vary with landings. In the economic model, analysed below, I shall consider only this case.

From comparison of Fig. 1 and 2, the difference in the law of diminishing returns for a non-self-regulating resource, and a self-regulating, density dependent resource, such as a sea fish population, may be readily appreciated. In the former case as other factors of production are added, i.e. as the effort is increased, the rate of increase of production diminishes, but the gross production increases monotonically toward some limiting upper value as an asymptote. In the case of the fish resource, the rate of increase of production diminishes continually with increasing effort also, but, in addition, after a certain level of effort is reached, the gross production falls off as well. In the extreme case

the resource, and production from it, could be reduced to zero, although this does not often happen in practice due to the cost of effort, which will be discussed below.

ECONOMIC MODEL OF THE FISHERY

To complete the economic model of the fishery, in order to investigate some of its properties, we need to consider, in addition to the foregoing, the cost of the fishing effort. The unit costs of the factors of production in a fishery are largely determined by the general economy, so we should not be making any very serious departure from reality, if we assume with Gordon (1954) that the cost of the fishing effort, C , is directly proportional to the amount of effort.

$$C = aE \quad (9)$$

where a is the cost of a unit of effort.

If we consider the simple case where the unit value of the catch is constant, and equal to β , we then have with the aid of (9) and (8) (combining some constants in 8 for simplicity of notation), for a complete model

$$\begin{aligned} L &= aE(b - E) \\ V &= \beta L \\ C &= aE \end{aligned} \quad (10)$$

We may now investigate some of the properties of this model.

As we have noted previously, the production function is a second degree polynomial, having a maximum at some intermediate value of fishing effort. This is shown as curve V in Fig. 4, where we have designated the amount of fishing

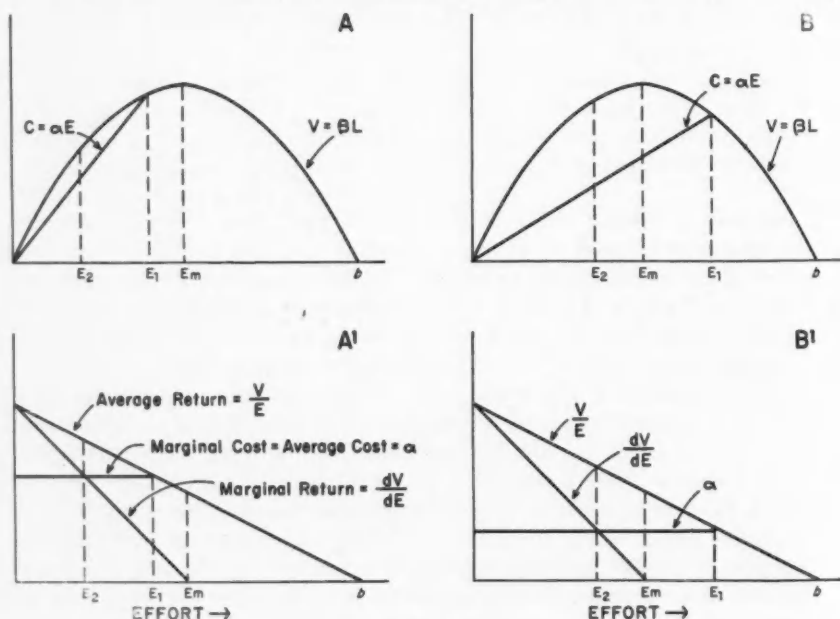


FIG. 4.

effort corresponding to maximum sustainable production by E_m . In this same figure, we show the cost function as the line C. We have in Fig. 4A and Fig. 4B illustrated two cases, first where a is so large that the amount of fishing effort (E_1), for which total cost equals total product, is less than E_m ; and second where a is so small that E_1 is greater than E_m .

The necessary condition for maximum production is, of course,

$$\frac{dV}{dE} = a\beta(b - 2E) = 0$$

whence

$$E_m = \frac{b}{2} \quad (11)$$

From the first two equations of (10)

$$V = a\beta E(b - E)$$

The average return is then

$$\frac{V}{E} = a\beta(b - E) \quad (12)$$

and the marginal return is then

$$\frac{dV}{dE} = a\beta(b - 2E) \quad (13)$$

while marginal cost and average cost are equal:

$$\frac{C}{E} = a \quad (14)$$

and

$$\frac{dC}{dE} = a \quad (15)$$

These functions are illustrated in Fig. 4, A^1 and B^1 , for the same two values of a as in Fig. 4, A and B.

It may be seen that marginal return falls to zero at $E = b/2$, which is also the amount of effort E_m for which total product is maximum.

The *net economic yield* is the difference between total cost and total product

$$Y = C - V = aE - \beta aE(b - E) \quad (16)$$

and will be maximum for that value of effort where

$$\frac{dY}{dE} = a - a\beta(b - 2E) = 0$$

or

$$a = a\beta(b - 2E) \quad (17)$$

$$E_2 = \frac{1}{2}\left(b - \frac{a}{a\beta}\right) \quad (18)$$

This is also, of course, the value of E for which the marginal cost equals the marginal return. It is labelled E_2 in Fig. 4.

In a fishery which is a common property resource, where anyone who wishes to do so is free to enter, new operators will be attracted to come into the fishery so long as the average cost is less than the average return (cost, of course, including all the costs of factors of production, including interest on capital investments and the normal entrepreneurs' fee), so that in the unrestricted common-property fishery the effort will grow until it reaches E_1 , where average cost equals average return and the net economic yield is zero.

For average cost equal to average return

$$a = a\beta(b - E)$$

so that

$$E_1 = b - \frac{a}{a\beta} \quad (19)$$

If unit cost is high relative to unit price of product (Fig. 4A, A^1), E_1 may be at a level of effort below that corresponding to maximum sustainable yield (E_m). In this case no increase in total yield can be obtained from restrictions on fishing effort. Any increase in yield must involve increasing unit prices or decreasing unit costs by some artificial means, such as price supports, subsidies, etc.

If, on the other hand, unit price is sufficiently high relative to unit cost (Fig. 4B, B^1), E_1 may be at a level of effort higher than the level E_m where maximum yield is obtainable. In this case, the yield can be increased by restricting the amount of fishing effort.

The maximum net economic yield will be obtained by restricting the fishing effort to E_2 . From (11), (18), and (19) it may be seen that this is always (1) at a lower level of fishing intensity than that at which maximum total catch is obtained (E_m) and, (2) at half the intensity (E_1) at which the unrestricted common-property fishery will arrive. Since E_2 is always less than E_1 and E_m , maximizing the net economic yield must always entail some sacrifice of total production.

If it is desirable to maximize the net economic yield, this may be accomplished, as has been advocated by Gordon (1953, 1954), by making the fishery a property right, under unified control, because in this event that intensity of fishing will result where marginal cost equals marginal return, which corresponds exactly, as has been shown above, to the condition of maximum net economic yield which, in this event, would be the rent from the property.

Under some circumstances, it may be desirable to reduce fishing effort below E_1 but yet not reduce it to E_2 . This, for example, is the case where, as in Fig. 4B, the uncontrolled common-property fishery will become so intense that the total catch is less than the maximum sustainable catch, and it is desired to maximize the sustainable catch. This may be accomplished by restricting the effort to E_m by suitable measures. If these regulations are so selected that the cost per unit of fishing effort is not increased, there will be some net economic

yield also, measured by the difference $V-C$ at E_m . Regulations in practice are often used such that the unit cost is increased at the same time the effort is restricted, so that the net economic yield is partly or completely dissipated.

SOME SOCIAL AND POLITICAL CONSIDERATIONS

Two of the possible benefits from fishery management are increased total production of food and other marine products, and increased net economic return to the fishermen. It may be seen that these are to some degree mutually exclusive, however. In the case of Fig. 4A, no increase in production can be obtained by curtailing effort, and an increase in net economic yield must entail sacrifice of some production. In the case of Fig. 4B, it is possible to increase production and at the same time obtain some net economic return by curtailing fishing effort, until it reaches the level E_m . Below E_m , however, again increased net economic return inevitably implies decreased production.

Gordon (1953) has strongly advocated managing a fishery to maximize the net economic return on the theory (p. 443) that, "... with every productive enterprise—the measure of its own contribution to human economic welfare is determined by its *net* output, after the costs of the factors necessary to that output's production have been deducted". He does, however, qualify this by noting "... the economic optimum is not necessarily the *human* optimum. Under certain circumstances we may well prefer to have an economically 'inefficient' fishery if the other effects of organizing the fishery along economically optimum lines are politically difficult or socially undesirable."

One of the important social considerations is the increasing requirement of protein food to feed the world's rapidly growing human population. The UNSCUR Conference in 1949 spent a great deal of time considering current food shortages, the prospective requirements in the near future, and means by which they can be satisfied. Broadley (1950), for example, pointed out that even before the Second World War food standards in many countries fell short of a minimum caloric diet, and fell even further short of minimum requirements of proteins, vitamins, and minerals. The forecast for 1960 indicated a very large increase in the requirements. It was indicated by other persons at the conference that a large increase in production from agriculture could be obtained by bringing land now sub-marginal into production, and by increasing the efficiency of agriculture. This, however, will quite obviously require great efforts both nationally and internationally, without much regard to the obtaining of a net economic yield from the increase of production. The existence of agricultural subsidies, direct or indirect, in many countries indicates the necessity of sacrificing some economic yield in order to obtain the production needed to feed the human population.

There is also some doubt whether the supply of proteins required can be produced on the land. Le Gall (1951) states, with respect to the world requirements of proteins: "The present annual needs are approximately 50 million tons; 75 million tons will be required by 1960, and the land alone will not be able to provide them."

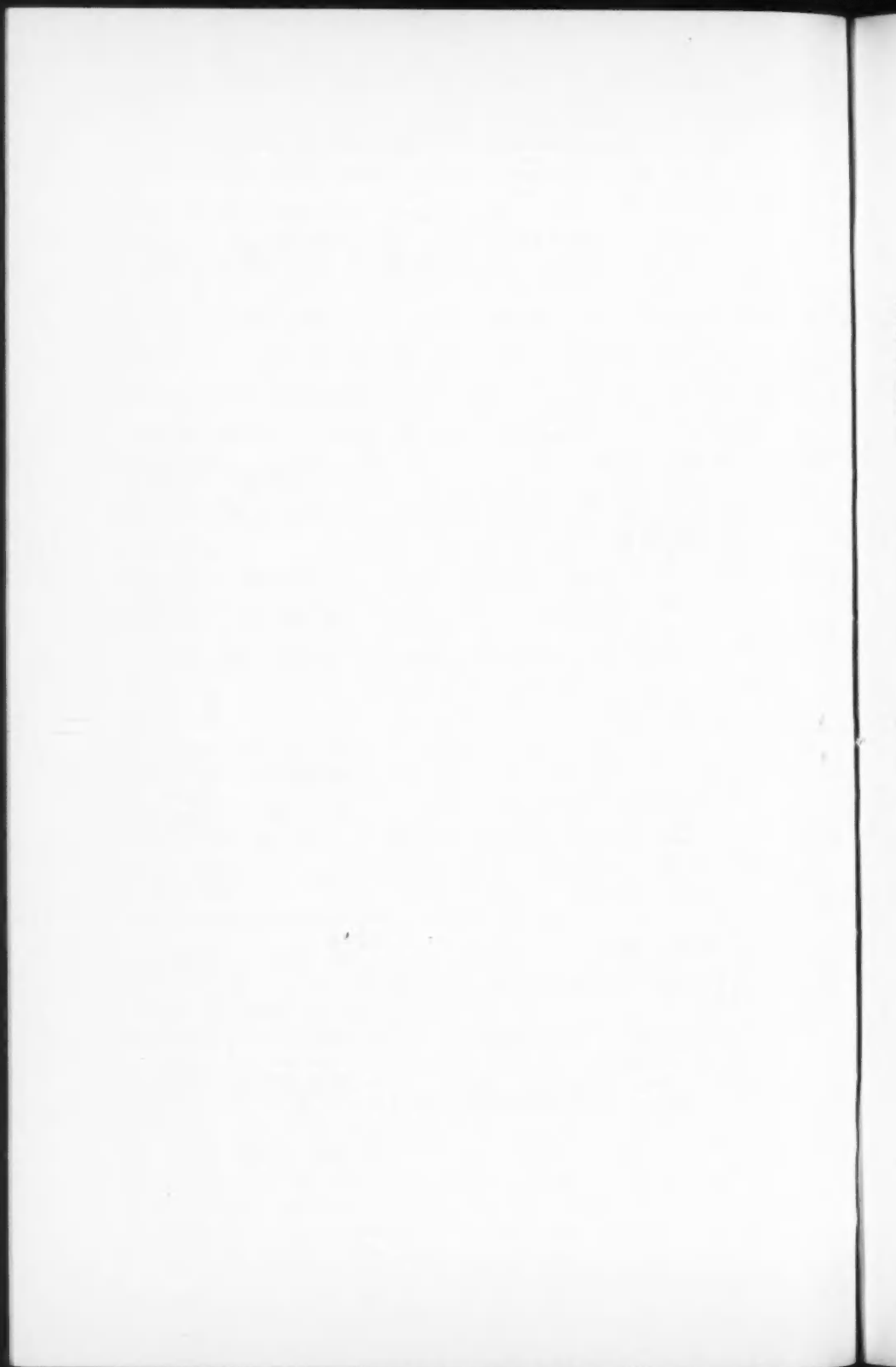
It would seem, therefore, that there is adequate reason to give first priority to maximizing the yield of the sea fisheries. This choice has been the basis of fishery management, in general, in the United States, and has, as noted by Graham (1956), been explicit in all the recent international conventions, in the New World. He also stated, that in the Old World there has not, as yet, been made any explicit choice among the possible qualities of the fishery. The conclusions of the recent United Nations Conference on the Conservation of the Living Resources of the Sea (see footnote on page 671) indicates, however, that all the nations in attendance are giving high priority to this alternative.

For the fisheries of the high seas, which are exploited by several nations jointly, there also arises the difficulty of applying any common economic criterion. The level of exploitation giving maximum sustainable production is a property of the fish population, and is the same regardless of who catches the fish. The maximum net economic yield, on the other hand, depends not only on the dynamics of the fish population, but also on the value of the catch and the costs of making the catch. Since the value of a given kind of fish varies from nation to nation, and the cost of a unit of fishing effort also varies from nation to nation, it is difficult to see how any common agreement as to the level of fishing effort corresponding to maximum net economic yield could be arrived at in an international, high-seas fishery. For this reason, even aside from the question of the social desirability, the economic yield appears, at this time at least, to be a quite impossible basis of agreement among nations for the joint management of the high-seas fisheries.

In a fishery such that, without regulation, the fishing intensity can exceed the level where the sustainable production is the maximum (Fig. 4B), the production can be maximized by curtailment of the fishing intensity. Such curtailment can be accomplished in a variety of ways, which leads to further problems of a social nature. If, in such a fishery, the fishing intensity is limited to E_m , the maximum average sustainable catch will be obtained. Some net economic return is also possible (the difference $V-C$ at E_m), provided that the cost per unit of fishing effort is not increased. This, however, involves, in one way or another, establishing at least a limited property right in the fishery, because, if it remains open to exploitation by all-comers, with only the total annual effort being limited (as, for example, by the establishment only of annual total catch limits, as in the North Pacific Halibut fishery) there is a tendency for additional participants to enter the fishery, decreasing the length of the season, or the amount gear fished per vessel, with a consequent increase in unit costs, dissipating some or all of the economic yield. It has been argued by Nesbit (1943) and others that the net economic yield should be preserved by a preferential licensing system, or other means of limiting the number of persons engaged in the fishery. This, however, comes into conflict with another possible benefit from fishery management, the providing of maximum opportunity for employment in the fishery. Many social and political considerations enter into the choice involved here. It is not my purpose to attempt even to review these considerations, but merely to point out that free access to the fishery by all citizens and the obtaining of the possible economic yield are mutually exclusive.

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The Optimum Level of Fisheries Exploitation^{1,2}

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IN a thoughtful and interesting article, Dr. Schaefer [1] rightly emphasizes the importance of the dynamic relationship between fishing effort and yield and corollary economic implications, and of the long-run point of view. After making allowances for semantic difficulties, he is, I believe, in substantial agreement with Professors Scott and Gordon and, with a more precise definition of cost of production, from the viewpoint of society rather than from that of private enterprise, he would find that their analyses have covered many of the points that he has raised.

The law of diminishing returns as applied to the fisheries has been discussed quite thoroughly by Professor Gordon³, who concluded that any one of three factors—the law of diminishing returns (in the true sense), population-reduction effects, or market price effects—could result in a landings (value) function with the necessary negative second derivative (decreasing marginal returns) to produce a stable equilibrium level of exploitation [6]. Productive resources or services are employed in varying combinations, and the law of diminishing returns (in current usage, the law of variable proportions) states that, if the quantity of one service or resource is increased in relation to all of the others in the combination, after a certain point equal additional increments of input of that service or resource will be rewarded by diminishing increments of product. An increasing fishing effort (which is itself a "basket" of varying factors—labour-time, labour-skill, capital goods of different sorts) will, in combination with a "given" fish stock or "population", arrive eventually at the point of diminishing returns. If the increase in effort has also a secondary effect in reducing the fish stock, so that landings are reduced still further, that is a reduced-population effect, not the law of diminishing returns⁴.

It is debatable whether there is a "fundamental fertility" of the land in any different sense than there is a "fundamental" fish population in the sea. Both may be depleted by over-exploitation so that future yields are reduced. There appears to be no point in attempting to classify resources as renewable or non-renewable (except to distinguish, as Marshall [7] did, between royalties and rents). Non-

¹Received for publication March 11, 1957.

²Comments on a forthcoming article by M. B. Schaefer [1] and on earlier discussions by H. S. Gordon [2, 3] and Anthony Scott [4].

³In [2] and [3]; see also [5].

⁴If over-exploitation results in a stable population equilibrium at a lower level, the situation might be diagrammed as a lowering of the landings curve L and of the asymptote Oa that it approaches (Gordon [2], p. 444, fig. 1), rather than the situation illustrated by Gordon (p. 455, fig. 8) in which the landings function L reaches a maximum and then declines because the average size of fish is reduced by fishing.

renewable resources are depleted by exploitation; renewable resources are depleted, at least temporarily, by over-exploitation; the decrease in both cases represents a cost of production to society. Thus, the present value of reductions in future yield resulting from over-exploitation must be added to cost of production in attempting to compute the economic optimum level of exploitation of the fishery. (This does not make the determination of the optimum any easier. A neo-Malthusian might set a high value on future production and consequently on the cost of over-exploitation, while others might view the matter more optimistically.)

Professor Scott has dealt with this question as a problem of the maximization of net returns in a situation of sole ownership of the fishery [8]. In the short run, the sole owner would seek to maximize his net returns by exploitation of the fishery up to the point where marginal cost equals price. For the long-run, he would try to arrange for the optimum series of landings through the future—to maximize the present value of the fishery (the present value of the discounted net returns of future periods)—by fixing output at the level where marginal user cost equals current marginal net revenue. User cost would include not only cash costs and opportunity costs, but also the (positive or negative) present value of future changes in the value of landings caused by the current extent of exploitation.

The current cost of future changed-population effects on landings is, accordingly, dependent upon two things: first, the amount of future decreases (or increases) in the value of landings resulting from the current scale of exploitation, and second, the rate of interest (or the owner's rate of time preference) at which such expected changes in value are discounted to the present.

Professor Scott has also indicated [9] wherein the social optimum equilibrium level of exploitation might coincide with that of sole ownership. Such would be the case in a world of perfect competition in the economic sense, where there is perfect knowledge of the market for goods and services, prices and the mobility of resources are not restricted, and no economic unit is large enough relative to the market to exert any perceptible influence on it. Under such conditions, society or the sole owner would utilize productive resources in the fishery only up to the margin at which the net return to such resources would be no less than that which they could obtain in another industry (i.e., the "opportunity costs" of resources would be equal in all uses).

Maximization of net economic yield as a social objective implies the assumption that the market prices of fish products and of all other goods and services indicate the relative value placed upon them by society and hence provide a valid basis for determining the optimum allocation of resources in production. If a man can get a higher return for his labour and capital in a pretzel factory than in the halibut fishery, then society is voting, in terms of the value placed on the product, for more pretzels instead of more halibut. If, in future, the necessary proteins cannot be produced on land, then the need for additional proteins will be reflected in higher fish prices relative to prices of other foods and other goods and services, causing an increased flow of productive resources into the fisheries.

Expansion in the fisheries would be limited by several factors, if operative: the competition of other uses for productive resources would tend to cut off expansion at the point where their marginal returns in the fisheries are no greater than in other uses, and marginal returns might themselves be reduced by diminishing (catch) returns per unit of effort, by reduced-population effects on catch, or by the effect of increased supply in lowering market prices.

Choice of the maximum economic yield as a social welfare optimum implies also, of course, the assumption that perfect competition exists and that the existing income distribution is accepted. But neither competition nor income distribution is perfect, and in recognition of that fact, society employs various measures for the re-distribution of income or of costs—production subsidies, progressive income and inheritance taxes, pensions and other social security payments, and international loans and gifts to increase consumption and promote industrial growth in economically underdeveloped parts of the world.

However, vague objectives such as "the maximum sustained yield" or "a maximum supply of food", and "providing the maximum opportunity for employment in the fishery" ignore completely questions such as the value set upon such production by society and the costs of production involved—i.e., the allocation of its productive resources by society so as to obtain the maximum net (value) product. Of what use to set production objectives that cannot be realized for lack of the effective demand necessary to call forth the production? The undernourished (and the well-nourished) millions of the world will enjoy the maximum physical yield from the world's fisheries only if their demand can be mobilized in terms of purchasing power to pay fishermen to catch the fish, and moreover, only if exploitation of the fisheries up to that point will yield more product value to the marginal units of productive resources than could be realized in other forms of production.

Providing a maximum opportunity for employment in the fishery is not a valid objective of management policy, if it be accepted that social welfare is best served by facilitating the flow of productive resources, including labour, into the most (value) productive uses. Professor Gordon has explained why fishermen tend to accept lower remuneration for their work than they could obtain in other occupations (i.e., why "opportunity costs" are lower in fisheries production). If there are intangible benefits in a fisherman's life that enable him to accept a lower material reward than he could obtain elsewhere, those social benefits in effect reduce the cost of fishing to society.

Granting that the maximum economic yield does not always coincide with the social welfare optimum as an objective of policy, it would be well, before concluding in any specific instance that the economic optimum does not serve the best interests of society, to make sure that all of the economic factors have been taken into account to arrive at the true maximum net yield to society. For instance, the fact that the lobster or the halibut fishery is complementary to other fisheries or other occupations might justify a somewhat larger entry of fishermen, boats, and gear than could be justified on the basis of net economic yield in the one fishery alone. But the problem is complex: the maximum economic yield to

society might only be obtainable from year-around fishing for the one species by a smaller number of fishermen, if control measures could be devised to limit entry to the optimum number.⁵

Dr. Schaefer has correctly pointed out that the maximum net economic yield, aside from the question of social desirability, appears to be a quite impossible basis of agreement among nations for the joint management of the high-seas fisheries. It may be unnecessary to add that social welfare also has different regional, national, and international aspects. Agreement on humanitarian standards and welfare objectives, and the reconciliation of these with regional or national interests, are not the least of human problems. Maximizing net economic yield from the world standpoint would mean the absolute freedom of labour and capital to move to the richest natural resources, wherever they might be. Thus would there be an approach, not only toward the maximum production of wealth, but also toward world-wide equalization of the returns to labour-time and labour-skill. We have come part way toward the acceptance of this "opportunity cost" equalizing principle within national boundaries, but there are substantial reasons why few in the wealthier countries are willing to go very far towards implementing it on the international level.

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- [6] Pages 129-130 and 137-140 of Gordon [3].
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- [8] Section III of Scott [4].
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⁵With a limited entry of fishermen, the better fishing grounds would yield an economic rent. Under a situation of private ownership of the fishery, this would accrue to the owner. Under public ownership and management, the rent (or some part of it) could be captured for society by sale of fishing licenses to the highest bidder or by some other method of taxation on those exploiting the fishery. Professor Gordon has discussed alternatives, noting that the proceeds of the tax could be redistributed to the fishermen, if desired (page 457 of [2]). There would be serious objections to such a transfer from the standpoint of both ethics and economics. Production effects, if any, would probably operate in a direction away from the economic optimum envisaged by limitation of entry into the fishery; for the most part, the fisherman would merely anticipate receipt of the bonus by raising his bidding price for a license or share of a quota, in order to qualify as one of the privileged few recipients. On ethical grounds, it would be difficult to justify government redistribution of income to a vested interest rather than on the basis of some criterion of social equity or welfare.

Permanence and Size of Home Territory in Stream-Dwelling Cutthroat Trout¹

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ABSTRACT

Gorge Creek is a small cutthroat trout stream in Alberta on the eastern slopes of the Rocky Mountains. In the summer of 1954, 98 trout were tagged with Petersen tags, weighed and returned to the pool of capture. In the same summer and in the next two, 58 of these trout were recaptured, some several times, so that, altogether, 83 records were obtained. Twenty-three records are of the first year, 35 from the second and 25 from the third.

Sixty-seven per cent of the recaptures were made in the original pool or less than 200 yards from it. Of the remaining 33%, one fish had moved 1.5 miles upstream and remained there. The others had all drifted downstream. The drifters were smaller fish than those that stayed home, and they either lost weight or gained at rates considerably below normal. It is suggested these fish had been injured by the tags. The general conclusion is that each cutthroat trout of Gorge Creek has a home territory not over twenty yards long and that the whole life is spent in it.

INTRODUCTION

For many years the management of fisheries has been treated largely as a statistical problem, and the fishes dealt with as large groups such as recruits, breeding population, catch. The lakes and streams have been studied as areas providing food and cover for a certain population of fish, expressed as pounds per acre or kilograms per hectare. While these approaches have undoubtedly led to much valuable knowledge about fishery management, there remain a number of problems where progress has been decidedly slow. Perhaps the outstanding example is the problem of the proper use of hatchery-raised trout for stream stocking. Despite adequate carrying capacities and apparently suitable environmental conditions the survival of hatchery stock in streams has been generally low. The fact that stocking has been highly successful in a few places serves mainly to point up the general problem.

In the past few years a fruitful new approach to this puzzle has been provided by the students of behaviour. More and more aquatic biologists are realizing that it is going to be extremely profitable to begin studying fish as individuals rather than as statistical quantities. The clear demonstration that a social order exists among trout in a section of stream, and that they possess strongly aggressive territorial behaviour (e.g., Newman, 1956), immediately suggests an explanation for the well-known drifting of planted hatchery trout. Gerking's review and account of his own experiments on two Indiana streams (Gerking, 1953) shows that home territory is quite a general aspect of the behaviour of stream fishes. Allen (1951) has demonstrated a marked tendency

¹Received for publication March 14, 1957.

for individual brown trout to inhabit only a limited section of their stream; he postulates that the stream population actually consists of a linear series of discrete non-mixing populations. The present author (Miller, 1954) showed that cutthroat trout, when removed from their homes and liberated elsewhere in the same stream, made considerable effort to return. This urge to "home" persisted even after several weeks forcible retention in a new locality.

The present study offers further evidence that stream-dwelling cutthroat trout have homes; the homes are shown to be quite small stretches of stream that are occupied for at least three years, presumably for life.

Gorge Creek, the test stream of the Alberta Biological station, was used. This is a small cutthroat trout stream, typical of a large number of East Slope tributaries. The lower three miles (5 km.) have been used for some years for studies of survival of hatchery-raised trout. The upper three miles have been little disturbed and no public fishing is permitted. This section varies from 15 to 30 feet (5-10 m.) in width and has a gentle gradient producing a current of 1.5 to 7 miles per hour (2.4-11 km./hour). It flows through steep shale banks and has carved numerous deep, rocky pools. It carries a population of small cutthroat trout, estimated roughly at 1,000 per mile (620 per km.). There are no other fish.

In earlier experiments (Miller, 1954) a series of pools were numbered and the distances between them roughly determined by pacing. In the present experiment pools 31 to 38, extending over 660 yards (600 m.) of stream were used. During the summer of 1954, 98 cutthroat trout were caught by fly-fishing, given numbered plastic Petersen-type tags, weighed to the nearest quarter-ounce (7 g.) and released in the same pools in which they were captured. In 1954, 1955 and 1956 fly-fishing was carried out from May through September in the area of pools 31 to 38 and also for two miles above and four miles below. Recaptures of tagged fish were made during all three summers. As natural mortality probably has reduced the 98 to a small number, further returns will be few, and for that reason the study has been declared completed.

YEARS OF RECAPTURE

Ignoring fish that were caught less than one month after tagging date, 58 of the 98 trout have been recaptured, some several times. The years of recapture are shown in Table I.

TABLE I. Recaptures of tagged trout according to years of recapture.

Recaptured in year:	Number
1 only	7
1 and 2	11
2 only	15
1, 2 and 3	1
2 and 3	8
1 and 3	4
3 only	12
Total	58

Table I includes only one record for each fish, i.e., only the first recapture after tagging. The actual number of recaptures may be determined from the table by adding all records for each year. Thus in year 1, $7 + 11 + 1 + 4 = 23$ recaptures were made; in year 2, 35; and in year 3, 25. The total number of recaptures was 83.

EXTENT OF MOVEMENT

Of the 58 trout that supplied recapture information, 32 or 55%, were taken only in the pools in which they had been tagged—the home pools. If one considers the total number of recaptures (rather than the actual number of fish involved) the picture is not changed; thus 45 (54%) of the 83 recaptures were made in the home pools.

The likelihood of a recapture being made in the original pool of tagging decreased with time. This is demonstrated in the following summary:

Recaptures in year 1 = 23 of which 17 were in home pool (74%)

Recaptures in year 2 = 35 of which 19 were in home pool (54%)

Recaptures in year 3 = 25 of which 9 were in home pool (36%)

At first glance this record suggests that there is a strong tendency for trout to remain in one place for a year, about an even chance of its staying or moving in a second year, and two out of three chances that it will move by a third year. However, an analysis of the records of the trout that moved reveals that there is much less likelihood of leaving the home pool than these figures suggest.

DEGREE OF MOVEMENT. A total of 26 trout was recaptured in places other than the home pools. Of these, 7 were found less than 200 yards (180 m.) from home, and each of these 7 was caught at least once more in the new location. It seems that these fish were away from home when tagged, and therefore they have been added to the group that didn't move. The total permanent residents becomes 39 or 67%. There remain 19 trout which were recaptured more than 200 yards away from home and which failed (except one) to establish permanent residence elsewhere, i.e., second and subsequent recaptures were in different places. The one exception was a trout which went upstream 1.5 miles (2.4 km.) and remained there. It is possible this fish had been displaced by a flood at the time of tagging. The 18 other fish all moved downstream; 11 were caught between 400 and 1,000 yards below home and 7 from one to three miles below home.

REASONS FOR DOWNSTREAM MOVEMENT. The sizes and weight records of 14 of the 18 downstream drifters show that these fish were smaller at tagging time than the stay-at-homes, and also that they were either losing weight (6 fish) or failing to gain at normal rates (8 fish). A comparison of these with 30 non-drifters is presented in Table II.

TABLE II. Comparison of sizes and weight gains of fish that remained at home and fish that drifted downstream.

	No.	Av. weight at tagging		Weight range	Gain in year 2	Gain in year 3
		ounces	grams	ounces	%	%
Drifters	14	1.9	54	1.00-3.25	14.7	12.2
Stay-at-homes	30	2.9	82	1.25-7.0	18.3	31.4

A reasonable interpretation of these data would be to assume that the Petersen tags bothered the smaller fish; the tags may have caused them to lose weight and strength to the point where they were easily displaced downstream at times of higher water. Newman (1956) studied the social order in a group of rainbow and brook trout in a stream. He found the larger fish held the best positions and that there was continuous competition for the favoured positions. These observations suggest that if a trout were displaced downstream it would be faced with a more or less alien community into which it could fit itself only by aggressive action. The small tag-weakened trout in Gorge Creek might be unable to win a position and so would continue to drift. The fact that all the drifters were downstream lends weight to this hypothesis; for had it been random dispersal, some upstream movement should have been found.

DISCUSSION

This experiment has shown that at least 67% of the recaptured trout in Gorge Creek were occupying a definite home territory. The information available on the remaining 33%, while not conclusive, does suggest that the trout involved had been affected by the tags so that their behaviour was not normal. It seems not unreasonable to conclude that, normally, the cutthroat trout of Gorge Creek (and, probably, other East Slope streams) occupy a limited home territory throughout life.

The size of this home territory is not large. The pools used in the experiment varied from 10 to 20 yards (9-18 m.) in length. The records give only the pool numbers; however, after three years of intensive fishing in the experimental area, the author and the students doing the fishing acquired very detailed knowledge of each pool and of the distribution of the tagged trout within them. For example, a certain tagged trout would always be caught by a particular boulder, another under a certain overhanging stump, another just below a small riffle, and so on. Further, these well-known trout were not caught at other localities, although care was taken to distribute the fishing effort evenly over the whole area. A conservative estimate of the size of the normal home territory is about twenty yards of stream, ten above and ten below the usual resting place.

The twenty yards of *Lebensraum* apparently serve to encompass all stages of the trout's life cycle; observations on Gorge Creek have shown that spawning occurs in the head of the home pool. The fry drop down after hatching and live in the shallow quiet water along the banks, frequently in cracks between stones. Very few drift far below the home pool. Areas in which the trout have been removed by poisoning have extremely low fry counts the next year—one or two per mile as compared to 1,000 per mile in populated sections. Such sections also regain adult trout very slowly. Poisoning a half-mile stretch below a populated area several years in succession shows that only from a dozen to about 50 trout have drifted down from upstream. Fish which are displaced by high water apparently return to the home pool as soon as stream conditions allow them to. Gerking (1950) marked nine species of warm-water fishes in Richland Creek, Indiana, and found that 75% of the marked fish recaptured after a flood were in the original locality of marking.

ACKNOWLEDGMENTS

I wish to express my gratitude to the Alberta Department of Lands and Forests for their continued support of the Alberta Biological Station. I am also indebted to several of my students who, as part of their duties as field workers, did the bulk of the fishing that yielded the returns used in this paper. Among these I should like to mention D. A. Boag, W. D. Wishart, W. Windsor, R. G. Miller, D. Sheppard and R. Schlick.

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Squid, *Illex illecebrosus* (LeSueur), in the Newfoundland Fishing Area¹

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ABSTRACT

Data from incidental trawl catches of squid by the research vessel, *Investigator II*, showed that distribution of *Illex* in the Newfoundland area was marked by a seasonal migration over the Grand Banks in early May, and northward and westward as far as Hamilton Inlet, Labrador, and inshore Newfoundland by August. Earliest occurrence inshore was in late June, earlier in recent years than heretofore. Comparative numbers taken on the Grand Bank in May and June in different years appear to indicate the abundance to arrive inshore later in each year. Annual abundance inshore varies, but years of scarcity do not appear to be cyclical nor need they indicate year-class failure. A correlation between abundance inshore and weather conditions may exist. Measurements during the inshore migration showed a regular and large increment of length and weight monthly until October. Female squid reached a greater size than males in the late season but weighed less than males at the same mantle length. Fin length was 35 to 40% of mantle length in *Illex*, compared with 53 to 63% in *Loligo pealii*. Many males taken in the late season had reached sexual maturity, but only two females captured on the Grand Bank in May, 1953, had reached equivalent maturity: these females had greatly enlarged nidamental glands.

Small squid taken offshore in 1946 to 1952 had been feeding mostly on euphausiids, but larger squid taken inshore had been feeding mostly on fish. In females 44% of the stomachs were empty, and in males, 50%.

Parasites found were tapeworm plerocercoids of *Phyllobothrium* sp. and *Dinobothrium* (*sensu lato*) sp., and occasionally a small larval nematode.

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INTRODUCTION

LITTLE has been published regarding the short-finned squid, *Illex illecebrosus* (LeSueur), in the Newfoundland fishing area. La Pylaie (1825) described the habits of this squid from observations at St. Pierre and proposed the name *Loligo*

¹Received for publication December 24, 1956.

piscatorum for it. It had already been described, however, by LeSueur (1821) as *Loligo illecebrosa*. It is found on the New England coast as well as in Newfoundland and the Maritime Provinces of Canada, although the common squid of the New England area is *Loligo pealii* LeSueur, which has a much longer fin compared with its mantle length than *Illex*. No records of *Loligo pealii* have been obtained for the Newfoundland area.

The genus *Illex* was erected by Steenstrup (1880) to include the closely related European form *coindeti* which is considered by some to be a subspecific form of *illecebrosus* (Bigelow, 1926; Grimpe, 1933).

Miss Nancy Frost and Dr. Harold Thompson of the Newfoundland Fishery Research Laboratory, collected data from samples of squid taken at Bay Bulls, at Holyrood, on the Grand Bank and from other areas in Newfoundland in the years 1930 to 1933. The results of their work were published in the annual reports of the Newfoundland Fishery Research Commission for 1932-1934, and some of their unpublished work has been available to us. Our own observations extend over the years 1946 to 1953.

DISTRIBUTION

The short-finned squid was reported by Verrill (1881) to range from Cumberland Sound (Kumlein's collection) to Cape Hatteras (Agassiz). Grimpe (1933) gave the range of this species as from south of Cape Hatteras to Newfoundland, Cumberland Gulf, Greenland, Iceland, and the Faroes. Voss (1954, 1955, and personal communication) reported it to be common in the Gulf of Mexico and the Caribbean in water over 150 fathoms in depth. Our records of its occurrence extend as far north as Hebron Harbour, Labrador (M. J. Dunbar and E. H. Grainger, personal communication), although, according to fishermen, squid were seldom taken inshore so far north in Labrador until recent years.

The seasonal population of squid in the Newfoundland area would appear to be very large. The migration shoreward begins with the appearance of small squid on the Grand Bank in May. They grow rapidly in the Newfoundland area, and reach a large size by October and November before they migrate offshore. Sometimes they may winter as adults on the Grand Bank before migrating presumably into deeper water to spawn.

Our distribution records of squid are mostly from incidental captures by the research vessel *Investigator II*, 1946 to 1952, during exploratory otter-trawling for groundfish (Fig. 1, 3). But commercial draggers have occasionally brought in specimens from the Grand Bank, and sampling of the inshore catch was done monthly, 1951 to 1953, from June to November. In Fig. 1 and 3, the quantity of squid per 10 hours' trawling has been arbitrarily assigned to a horizontal area of each map rectangle. The yield of squid indicated in the rectangles has been determined from varying fishing effort and this effort in actual number of hours trawled is shown in Fig. 2 and 4; the number of hours trawled has been given arbitrarily to a vertical area of each map rectangle. The small amount of fishing shown in rectangle 27J indicates a large number of squid; the actual number taken was comparatively high in this and adjoining rectangles, where greater

effort yielded somewhat greater actual numbers for the area represented by rectangle 27K than rectangle 27J. Also, these squid were taken in July when the migration had reached inshore areas and squid were in large numbers.

The early season captures of squid by the *Investigator II* in May to July were generally confined to the southwestern, southern and eastern edges of the Grand Bank, which were presumably under the influence of comparatively warm Atlantic water at the time. Few to none were taken in the shallower or more northerly areas of the bank, where arctic water is predominant at this time of year. However, large quantities of squid generally reach inshore areas on the east coast of Newfoundland by late June (earliest recorded at Holyrood—June 23, 1952), and by August they have reached many other places on the Newfoundland coast. In the late summer and autumn, although the greatest concentrations of squid appear to be inshore or near the inshore waters, some squid are occasionally taken on the banks (Fig. 3). The greatest concentrations of squid available to fishermen occur at the heads of bays such as at Holyrood and Dildo on the east coast, but schools may be encountered for many miles seaward. Nielsen (1891) reported, for example, that large numbers of squid were seen as far as 30 miles from land around the coast of Newfoundland. Commercial draggers and our research vessels report schools of squid occasionally seen far out on the banks. Undoubtedly, in years of abundance the numbers of squid in the area are very great, and when they are being taken inshore in large quantities by fishermen they may be jigged almost anywhere near the coast. Largest concentrations occur at the traditional squid-jigging grounds, where they arrive earliest in the season and remain latest. These squid-jigging grounds are usually quite small areas near almost every fishing cove.

As the season advances the migration of squid is shown by their appearance northward and westward. In Table I (mostly uncollated data from notes of N. Frost and H. Thompson) Holyrood is taken as the actual point of first appearance of squid inshore, Francois is considerably to the west on the south coast, Fogo is representative of the northeast coast at Notre Dame Bay and Conche is still farther north (Fig. 5). Presumably, the most reliable data for the first appearance of squid are those of first reported strandings, because, according to the experience of the fishermen, when squid first arrive on the inshore grounds they are not easily jigged.

The early season migration, which is quite rapid, would appear to be towards the coast from the east and south over the Grand Bank. The more distant areas of the range are reached within a month after the first squid strike inshore. Of course, migration within coastal waters may have become quite general by June, since the squid, undoubtedly, are in pursuit of capelin (*Mallotus*) not far off the coast by this time and the migration inshore in July and August may be a short distance movement (Frost and Thompson, 1932). However, very small squid appear inshore late in the season in southern areas only (questionnaire to fishermen), suggesting that these are coming in from the south, also.

Scarcity of squid in some areas is reported over long periods, as at places on the south coast for a few years after 1934, and on the west coast north of Bay

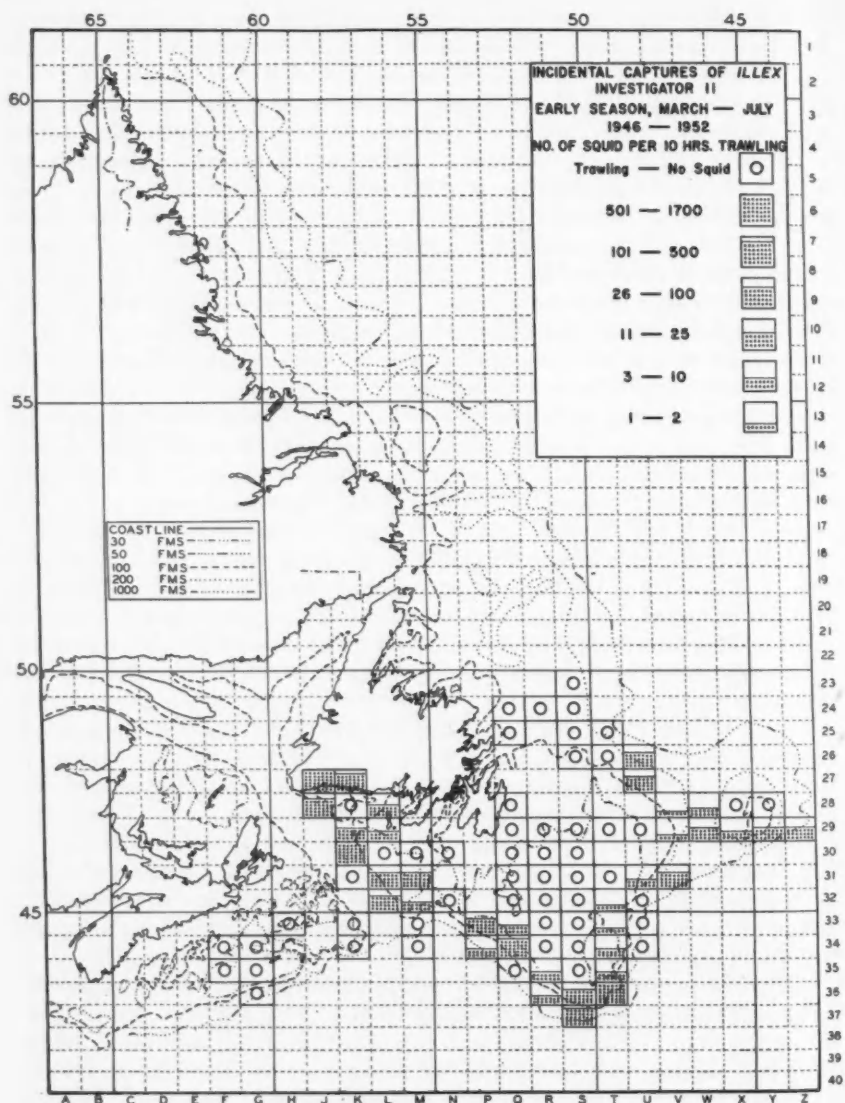


FIG. 1.—Early season captures of *Illex* incidental to exploratory trawling by the *Investigator II* in the Newfoundland area, 1946 to 1952. (Number of squid per 10 hours of trawling.)

of Islands. However, squid have appeared in great abundance in these areas. Records for some years show a very widespread appearance of squid throughout the area. Migrations even into the St. Lawrence estuary as far as Trois-Pistoles may occur as in 1930 (correspondence of Dr. H. Thompson with Professor

Georges Préfontaine, then of Laval University). But even in years of greatest abundance it is probable that temperature, turbidity, and other physical or chemical factors under the influence of local weather may cause sporadic appearances inshore in some areas. A record of observations at Holyrood during

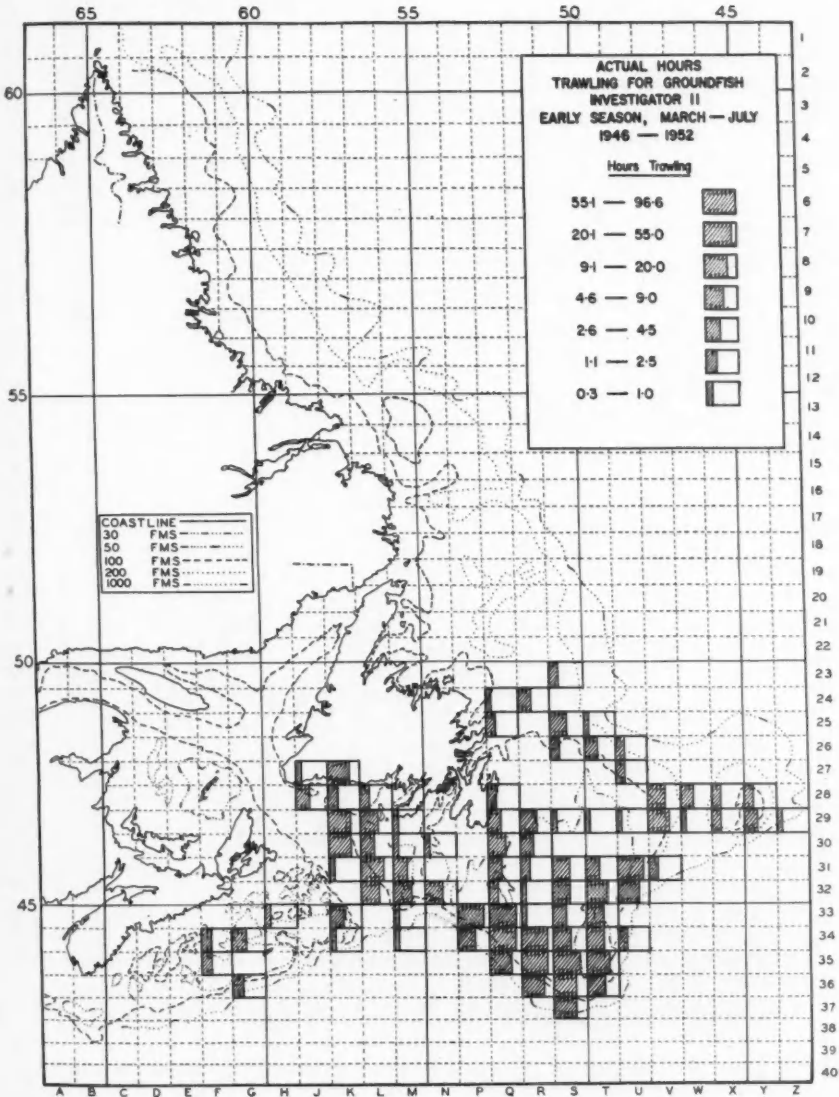


FIG. 2.—Actual number of hours of trawling by the *Investigator II*, January to July, 1940 to 1952.

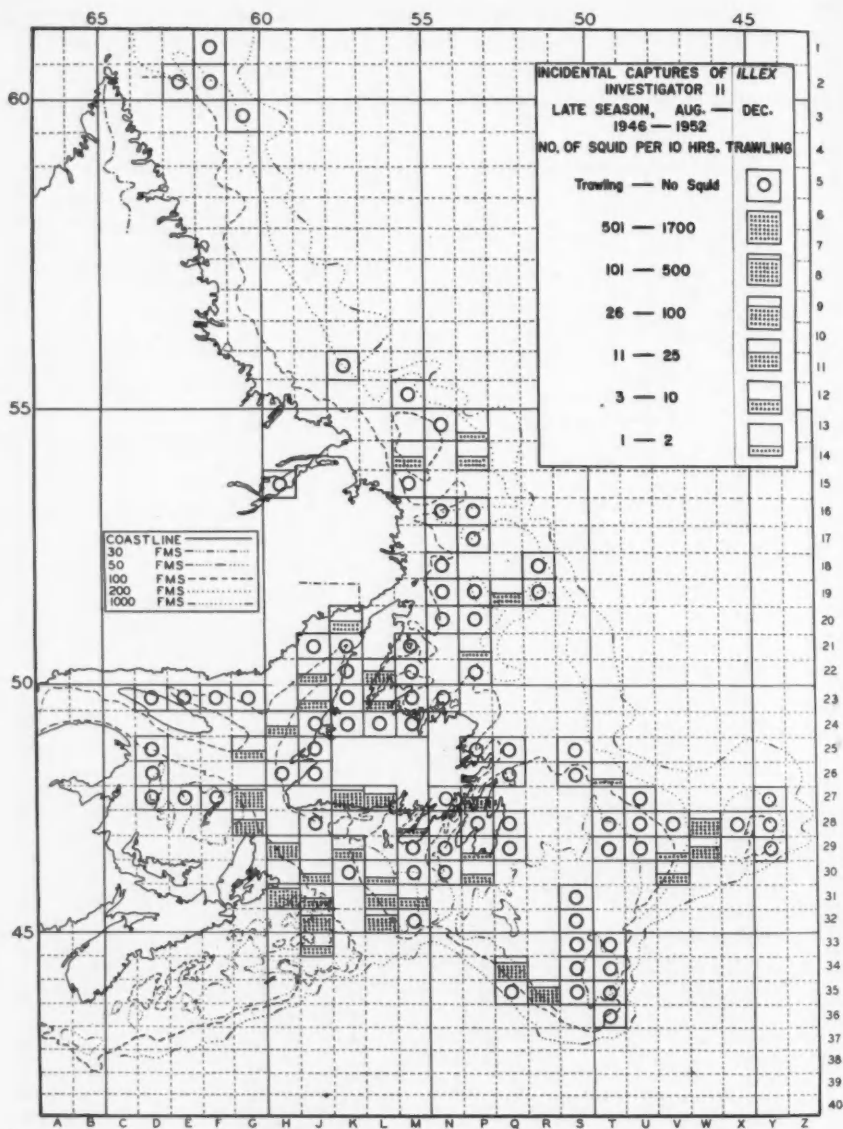


FIG. 3.—Late season captures of *Illex* (incidental to exploratory trawling) by the *Investigator II* in the Newfoundland area, 1946 to 1952. (Number of squid per 10 hours of trawling.)

the summer of 1952 (Table II) gives some evidence of the erratic appearance of squid. Generally, when the wind was onshore at Holyrood no squid were seen and none were jigged there (fishermen's observations). Fishermen reported a condition of turbidity of the water with onshore winds (which they called "dirty

water"); and, of course, the piling up of warm surface water with wind blowing onshore caused the temperature of the water near the land to rise in summer. One observation of the author made while squid-jigging was in progress, showed that when the wind changed to an onshore direction, almost immediately the

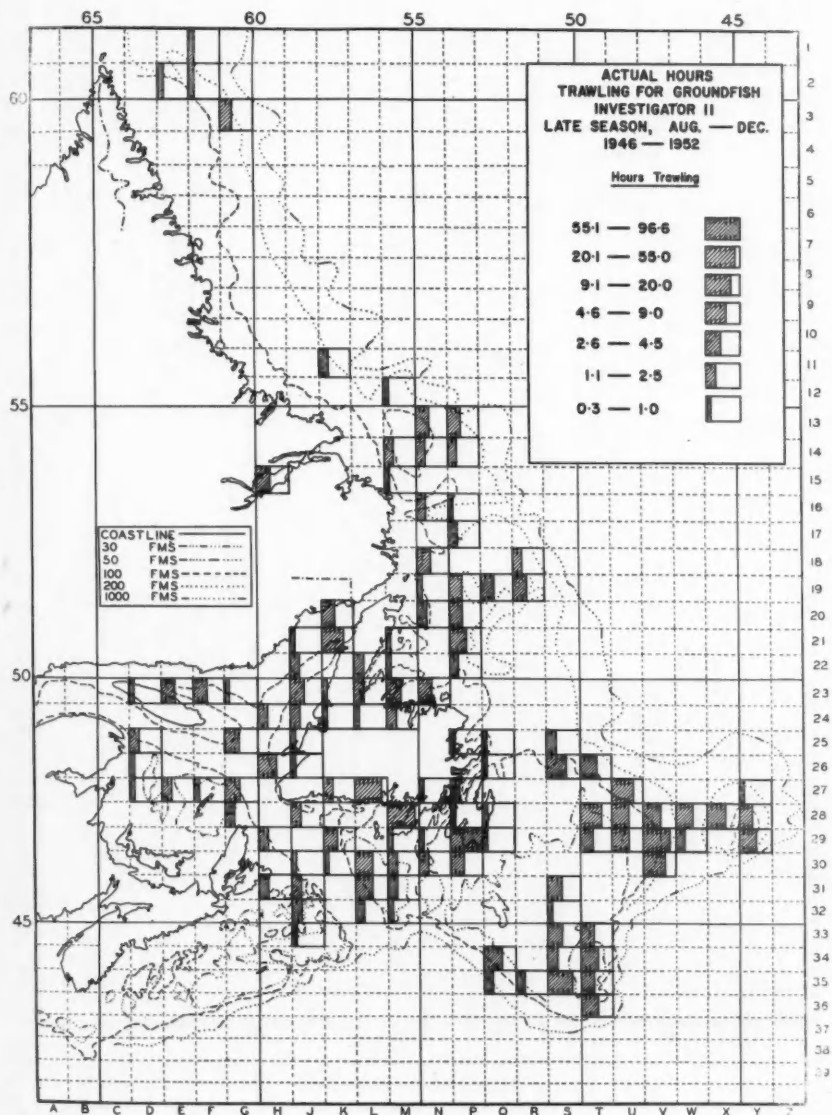


FIG. 4.—Actual number of hours of trawling by the *Investigator II* in the late season, August to December, 1946 to 1952.



FIG. 5.—Places in the Newfoundland area mentioned in the text. Numbered circles are *Michael Sars* stations, 1910.

TABLE I. Date of first reported seasonal occurrence of squid at Holyrood, Francois, Fogo and Conche or vicinity: east, southwest, northwest and north coasts, respectively.

Year	Holyrood	Observation	Francois or vicinity	Observation	Fogo or vicinity	Observation	Conche or vicinity	Observation
1929	July 22	Plentiful but not jigging	Aug. 6	Plenty in Burgeo Hr.	Aug. 19	Few seen with capelin	Aug. 30	Few seen
1931	July 14	Fairly plentiful, jigging	Aug. 14	Few jigged	Aug. 29	Few secured at Beaumont, N.D.B.	Aug. 18	First taken
1932	July 8	About 40 stranded	July 23	First jigged	Aug. 26	Plenty at Leading Tackles	Aug. 30	Plentiful
1933	July 17	About 40 stranded	July 20	Stranded, and in herring nets at Ramea	July 28	Fair amount seen	Aug. 8	First few jigged
1952	June 23	About 100 stranded	July 26	About 100 stranded at Brig Hr. Island, Labrador (L. M. Tuck)
1953	June 26	Millions stranded

TABLE II. Weather conditions and squid occurrence based on jigging at Holyrood, June to October, 1952. Times shown are Newfoundland Standard Time.

Date, 1952	Time	Sun	Wind	Water temp at surface	Condition of water	Jigging time	Result
June 25	6:55 p.m.	Just before sunset, clear	Offshore	2.0 °C.	Clear	30 min.	No squid
July 26	3:00	Bright	Offshore	14.4	Clear	Approx. 1 hr.	Many squid
Aug. 21	3:00	Bright	Onshore	19.0	Somewhat turbid (fishermen's opinion)	30 min.	No squid
Aug. 28	3:00	Bright	Offshore	14.5	Clear	Approx. 1 hr.	Many squid
Sept. 16	3:00	Dull	Offshore	12.1	Still somewhat turbid from on-shore winds (fishermen's opinion)	Approx. 1½ hr.	Few taken
Sept. 20	3:00	Bright	Offshore	11.8	Clear	Approx. 1½ hr.	Few taken
Oct. 20	3:00	Bright	Offshore	9.0	Clear	Approx. 1½ hr.	Occasional
Oct. 28	9:45	Moonlight	Offshore	8.9	Clear	Approx. 1 hr.	None taken by fishermen during day but sample of 90 jigged, at about 10:00 p.m.

squid seemed to leave the vicinity and no more were jigged while the wind continued in this direction.

Frost and Thompson (1932) postulated that favourable conditions of salinity and temperature on the southwest edge of the Grand Bank in spring (May to June) would allow a forecast of a large number of squid to appear inshore in the late season (August to October). This could not be demonstrated conclusively in subsequent years, perhaps because favourable conditions were difficult to define and not enough data could be obtained. However, the numbers of squid taken on the southwest edge of the Grand Bank in May or June appear to indicate the abundance of squid to arrive inshore in the late season (Table III). In years

TABLE III. Incidental early season captures of squid by the *Investigator II* on the Grand Bank, 1946 to 1952, and reported occurrence of squid inshore.

Year	Locality	Total hours trawling	Percentage trawling time productive of squid	No. of squid per 100 hours trawling	Reported inshore occurrence of squid later in year
1946 (May and June)	SW. & S. Grand Bank	81	10	385	Moderate numbers
1947 (May and June)	SW. & S. Grand Bank	91	3	70+ hundreds seen escaping from net	Very abundant
1948 (May and June)	SW. & S., N. & E. edge Grand Bank	67	1	3	Scarce
1949 (June only)	SW. edge of Grand Bank	31	0	0	Few
1950 (June only)	N. & NE. edge Grand Bank	24	14	95	Moderate numbers
1951 (May only)	SW. & S. Grand Bank	21	42	5,683	Very abundant
1952 (May and June)	SW. edge Grand Bank	22	21	3,523	Abundant

of scarcity, such as 1948 and 1949, very few squid were taken on the banks in the early season, while in years of abundance inshore such as 1951, many squid were taken in May on the southwest edge of the Grand Bank (in 1951 and 1952 the nets were fished with a cod-end lined with shrimp netting).

The temperature preference of *Illex*, stated provisionally by Frost and Thompson (1932) to be 7° to 15° C. near the surface inshore, was substantiated by our observations at Holyrood (Table II). However, our records of bottom temperatures when squid were taken on the Grand Bank were 0.5° to 8.0° C. (Table IV), lower than the 2° to 9° C. temperature preference of squid offshore suggested in Frost and Thompson's paper. However, it is difficult to say whether the temperatures at trawling depths represent where squid were taken by the

TABLE IV. Depth, bottom temperature and number of squid taken incidentally by the *Investigator II*, mostly on the Grand Bank, 1947 to 1950.

Bottom depth fathoms	Temperatures, degrees Centigrade							
	0.5-1.0	1.1-2.0	2.1-3.0	3.1-4.0	4.1-5.0	5.1-6.0	6.1-7.0	7.1-8.0
30	2	...	1
40	2	0	...	0
50	...	19	10	0	12	0
60	27	0	0	0	0	0	...	53
70	0	0	4	0	0	12
80	1	6	0	0	2
90	0	0	0	5	0
100	1	2	0	10	7
110	0	0	0	0	6
120	1	0	1	1	0
130	...	1	0	0	1
140	...	2	1	1	14
150	...	0	0	1	0
160	...	16	2	0	1
170	6	0
180	1
190	2
200	1

otter trawl, since the net was open when it was brought up at the end of the tow and some squid may have been taken in midwater or near the surface. Bottom depths in places where squid were taken by trawling ranged from 30 to 200 fathoms.

Illex larvae have not been taken in the area south of Newfoundland. The stations occupied by the *Michael Sars* North Atlantic Deep-Sea Expedition, 1910 (Fig. 5; No. 70 to 80 on the Grand Bank, June 30 to July 11, 1910, and No. 66 to 69, June 26 to 29, 1910, immediately south of the Grand Bank near 40° N. latitude, and at depths ranging to 2,200 metres) yielded a number of cephalopod larvae, none of which, however, were referred to *Illex illecebrosus* (Chun, 1913). Some squid larvae taken at station 67 belonged to the family Ommastrephidae, genus *Rhynchoteuthis*. The stations may quite possibly have been occupied too early in the summer for captures of larvae of *Illex*.

RELATIVE ANNUAL ABUNDANCE

The histogram of annual abundance of squid inshore in Newfoundland (Fig. 6) was constructed from records obtained as follows: in the years 1879 to 1911, from newspaper reports (a number of reports throughout the season—August to October); in 1912 to 1929, from annual reports of the Minister of Marine and Fisheries, Government of Newfoundland; in 1930 to 1934, from the Newfoundland Fisheries Research Commission annual reports; in 1935, from newspaper reports; in 1936 to 1948, from annual reports of the Newfoundland Fisheries Board, and in 1949 to 1954 from the records of the St. John's Biological Station of the Fisheries Research Board of Canada.

Reports of squid occurrence inshore in Newfoundland, however, do not necessarily indicate fluctuations in the total numbers of *Illex* in the entire offshore

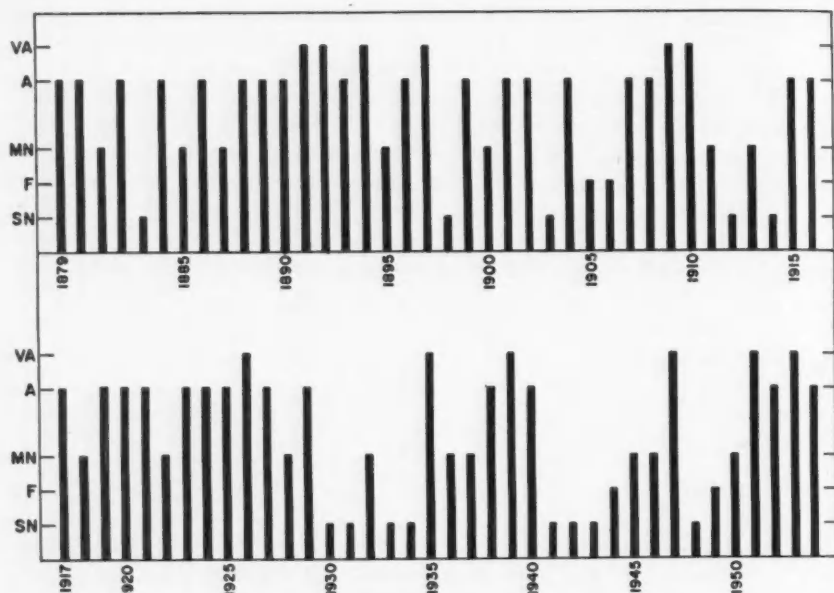


FIG. 6.—Relative annual abundance of squid in Newfoundland, 1879 to 1954 as indicated by reports of squid occurrence inshore. SN = scarce to none. F = few; MN = moderate numbers; A = abundant; VA = very abundant.

population. Fluctuations caused by success or failure of year-classes such as may occur in fish populations were suggested by Frost and Thompson (1933). However, since this squid very likely lays its eggs south of the Grand Bank, outside the influence of surface currents, in deep water where hydrographic conditions are approximately constant, birth and survival rates of squid may not vary greatly from year to year. The occurrence of squid inshore on the squid-jigging grounds may be at least partly dependent upon local weather conditions, and not entirely on the real abundance of squid in any year. In years of scarcity inshore, as in 1948 and 1949, small numbers of squid were taken on the banks in the late season by the *Investigator II*, and in years of abundance inshore correspondingly large numbers were taken on the banks during the late season (Table V). However, these late season figures of catch per unit effort show much less variation between years than the early season figures. There is probably less difference, therefore, between the numbers of squid on the banks late in the season than is suggested by their numbers inshore (Tables III and V).

Cycles of abundance or scarcity of squid can not be seen from our records although some correlation with cycles of climate and weather conditions may exist (Templeman and Fleming, 1953). Amelioration of climatic conditions may be causing an earlier appearance of squid inshore in Newfoundland in late years (Table I). The first occurrence of squid inshore, as shown by first strandings on

TABLE V. Incidental late season captures of squid by the *Investigator II* offshore, 1946 to 1952, and reported occurrence of squid inshore.

Year	Locality	Total hours trawling	Percentage trawling time productive of squid	No. of squid per 100 hours trawling	Reported inshore occurrence of squid late in year
1946 (July-Nov.)	Grand Bank St. Pierre Bank	29	36	14	Moderate numbers
1947 (July-Dec.)	Gulf of St. Lawrence St. Pierre Bank Banquereau Grand Bank	42	89	252	Very abundant
1948 (July, Aug.)	Gulf of St. Lawrence Grand Bank St. Pierre Bank	27	8	23	Scarce
1949 (July-Nov.)	Grand Bank St. Pierre Bank	128	1	2	Few
1950 (July-Dec.)	Hamilton Inlet Bank Off St. Anthony Gulf of St. Lawrence Grand Bank	37	29	151	Moderate numbers
1951 (July-Nov.)	Hamilton Inlet Bank Grand Bank	46	45	169	Very abundant
1952 (July-Nov.)	Hamilton Inlet Bank Laurentian Channel St. Pierre Bank	29	45	99	Abundant

the coast, was earlier in 1952 to 1954 than in the years from 1929 to 1933 (we do not have records of earliest occurrence in years previous to 1929, nor for the years 1934 to 1951). Abundance and scarcity, also, are relative terms in our records: even in years of so-called great scarcity such as 1943, the bait depots alone may handle as much as 400,000 lb. of squid (Table VI). Therefore, it seems that even in years when squid were reported as very scarce, they were

TABLE VI. Quantity of squid purchased by the Department of Fisheries or deposited by fishermen at bait depots in August, September and October from 1938 to 1944, and totals for 1949 and 1950, compared with the reported occurrence of squid in these years.

Year	August	September	October	Total—all depots	Reported occurrence of squid
	lb.	lb.	lb.	lb.	
1938	174,343	405,959	135,884	716,186	Abundant
1939	455,160	899,446	546,782	1,901,388	Very abundant
1940	394,071	165,440	569,192	1,128,703	Moderate numbers
1941	81,037	86,151	86,151	253,339	Scarce
1942	95,102	61,680	34,908	191,690	Scarce
1943	268,111	58,983	47,323	374,417	Scarce
1944	205,541	119,907	173,711	499,159	Few
1949	18,023	Few
1950	599,714	Moderate numbers

plentiful for short periods at certain places. Frost and Thompson (1933, 1934) showed how abundance of squid varied from place to place on the coast of Newfoundland in different years. The appearance of squid every summer and early autumn in large numbers near the coast where they may be jigged is an expected occurrence, and any year of scarcity on the east or south coasts is unusual and difficult to explain.

GROWTH

Squid which were taken incidentally to groundfish trawling by the *Investigator II* in the years 1946 to 1950 (about 300 squid in all) and shore samples (about 1,000 squid) as well as catches by the *Investigator II* in the years 1951 to 1953 (approximately 800 squid) are represented in the present study. Inshore sampling was done monthly from June to November in 1952 and 1953. Weights considered here were obtained from squid examined in 1952 only. Mantle lengths were measured, as by Frost and Thompson (1932), from the apex or tail end to the slight protuberance of the mantle edge at the neck, dorsally (anteriorly) (Fig. 7, A). A measuring board marked in half centimetres was used; and measurements were taken by placing the apex against the head end of the board. Lengths were estimated to the nearest millimetre where the mantle protuberance reached on the board. Fin lengths read at the time the mantle length was measured, were estimated to the nearest millimetre from the apex to the insertion of the fin (Fig. 7, B). In 1952, squid were measured and weighed fresh, and lengths in the fresh condition were used when available. Mantle lengths of squid preserved in formalin were generally somewhat less than those of fresh squid, but differences were less than 3% of total mantle length.

Measurements indicated substantial homogeneity in the population because (a) average lengths and weights of samples showed a regular month to month increase throughout the season in each year of observation (Table VII; Fig. 8, 9, 10) and (b) the modes of mantle lengths in samples taken concurrently in different areas were similar (Table VIII; also Frost and Thompson, 1932, 1933).

LENGTH AND WEIGHT INCREASE

Table VII and Fig. 8 and 9 of the mantle lengths and Fig. 10 of average weights of squid taken in each month show that size increases gradually throughout the season. Average mantle length almost doubles in this time, and average weight increases to almost 6 times the initial. In 1952 the percentage added to length and weight was approximately the same in each month until October, when it became considerably less. It would appear that maximum size was beginning to be reached in October in 1952; and in early November in 1951. Also, the larger squid apparently began to leave the area, making the smaller squid more prominent in the late samples. Templeman (1944) observed the same phenomenon in dogfish.

In November, 1952, a group of squid appeared which were smaller than normal for November (Fig. 9). In reply to a questionnaire, fishermen reported

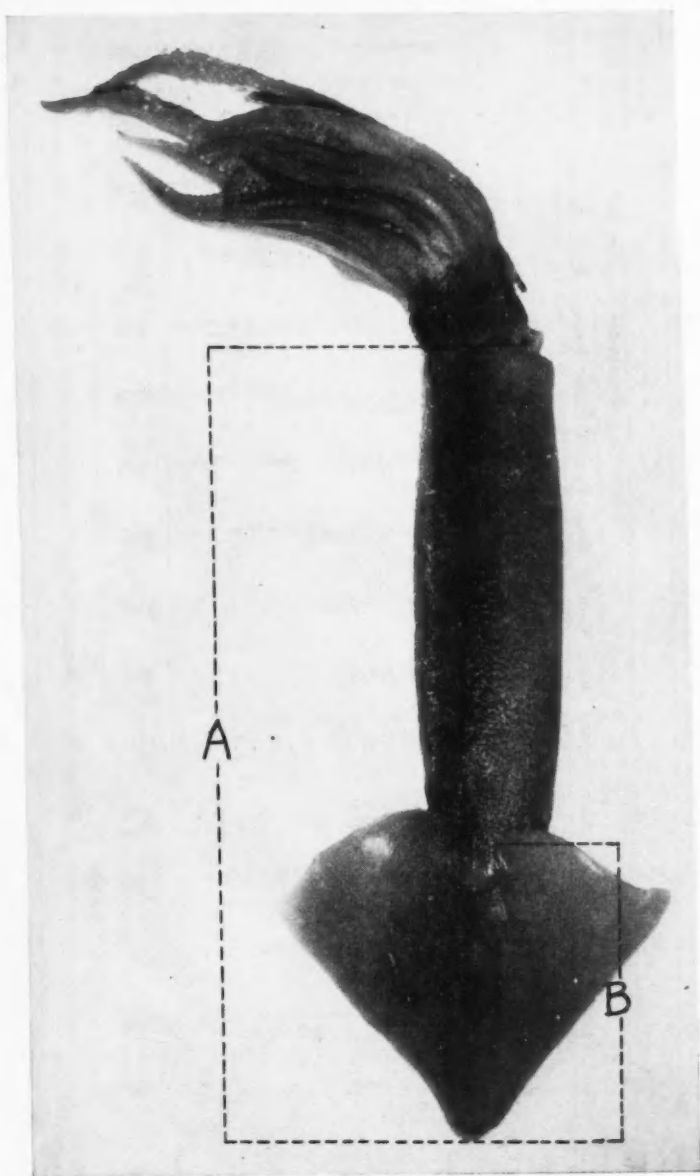


FIG. 7.—Mantle length, A, and fin length, B, of *Illex*.

TABLE VII. Mantle lengths of squid January, February, 1953, May to November, 1946 to 1953.

Mantle length	January to February		May		June		July		August		September		October		November (None later than 11th)	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
cm.																
10	4	2
11	16	4
12	24	11
13	31	26
14	49	46
15	62	42
16	21	25
17	7	9
18	0	3
19	1	1
20	0	0
21	1	0
22	3	0
23	2	0
24	2	1
25	1
26	0
27	0
28	1
29
30
Totals	4	8	216	171
Averages	20	23	14	14
Percentage monthly increase in av. length			24 ^b	27 ^b	14	21	13	12	17	11	10	19	4	4	4	-8

^aOctober 30, 1940, on the Grand Bank.^bAverage of 3 larger squid (1 male, 2 female) kept separate.

TABLE VIII. Comparison of mantle length frequencies of squid sampled concurrently from different areas in 1952. Samples from Chapel Arm were collected and measured by Dr. D. E. Sergeant.

Mantle lengths cm.	Holyrood (stranded) June 23	Grand Banks (trawled) June 30	Holyrood August 28	Chapel Arm August 22	St. John's Sept. 19	Holyrood Sept. 16 & 23	Chapel Arm Sept. 19
14	...	3
15	...	13
16	7	50
17	18	51	1	...
18	7	18	1	0	...
19	2	4	10	1	...
20	25	1	...
21	21	4	...	8	1
22	22	14	12	43	8
23	7	7	15	52	14
24	5	5	33	59	9
25	3	1	11	42	6
26	2	16	15	10
27	1	7	13	3
28	1	11	2
29	1	3	...
30	0	1	...
31	1	1	...
Number of squid	34	139	94	34	97	251	53
Average mantle length—cm.	17.1	16.6	21.2	22.9	24.4	24.0	24.2
Standard deviation	0.81	1.00	1.52	1.48	1.69	1.94	1.74
Standard error	±0.14	±0.08	±0.16	±0.25	±0.17	±0.12	±0.24

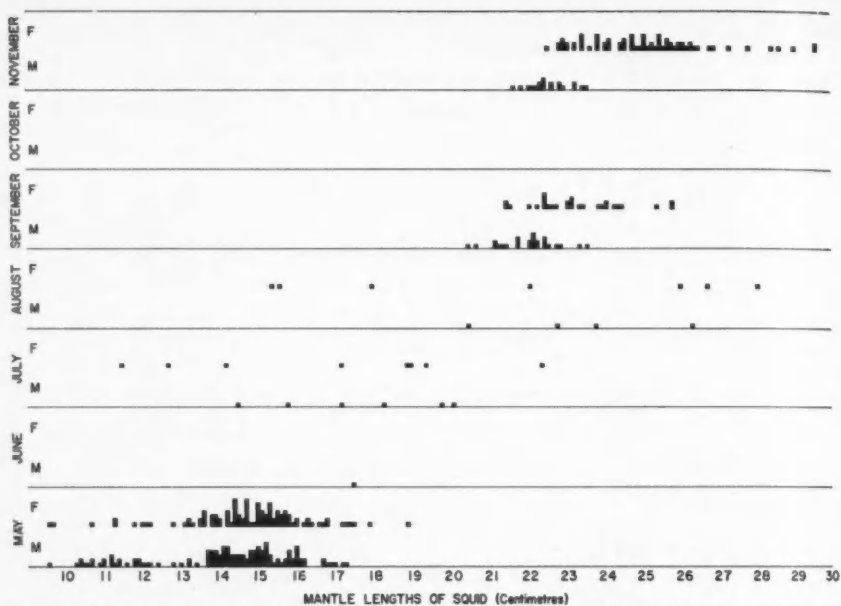


FIG. 8.—Mantle lengths of male and female *Illex* taken at Holyrood, Newfoundland, May to November, 1951.

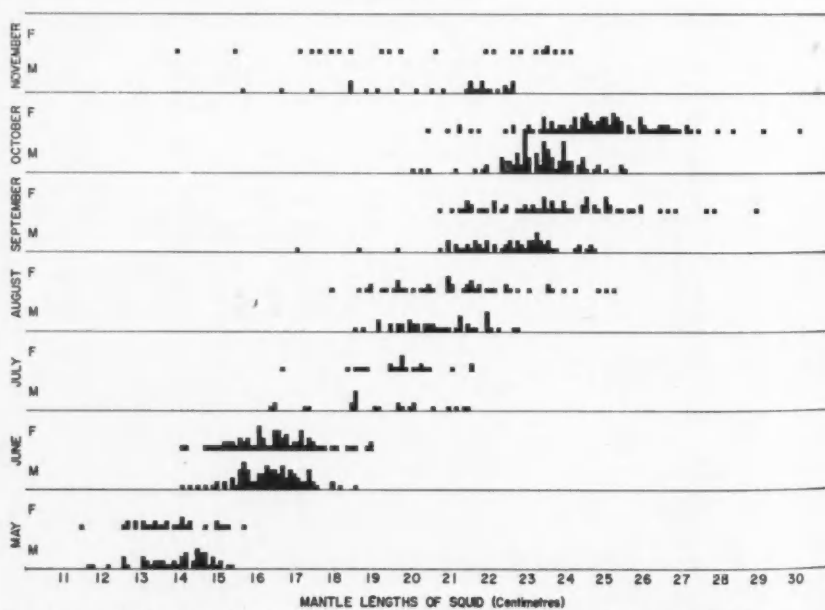


FIG. 9.—Mantle lengths of male and female *Illex* taken at Holyrood, Newfoundland, May to November, 1952.

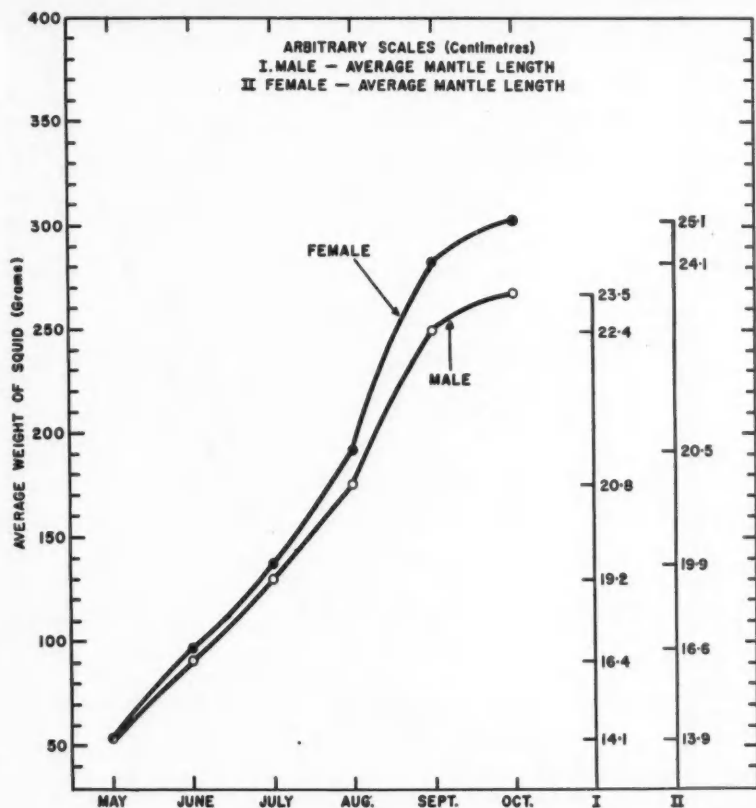


FIG. 10.—Average weight and mantle length of male and female *Illex* taken at Holyrood, Newfoundland, in each month, 1952.

that small squid have been present in considerable numbers late in the season inshore in some years. This was reported only in the more southerly parts of Newfoundland. The *Investigator II* also has occasionally taken small squid on the Grand Bank late in the season. It would seem, therefore, that these small late-season squid invaded the area from the south in some years.

SIZE DIFFERENCE BETWEEN THE SEXES

Males and females showed differences in average mantle length and average weight. In the 1952 samples no apparent differences were present in the May and June captures, but in July (average length of both sexes—20 cm.) the males were heavier for their length than females. Weight differences became more apparent as the season advanced and at larger sizes of squid. However, the females were larger than males (Fig. 11); they reached this considerably greater size in September and October.

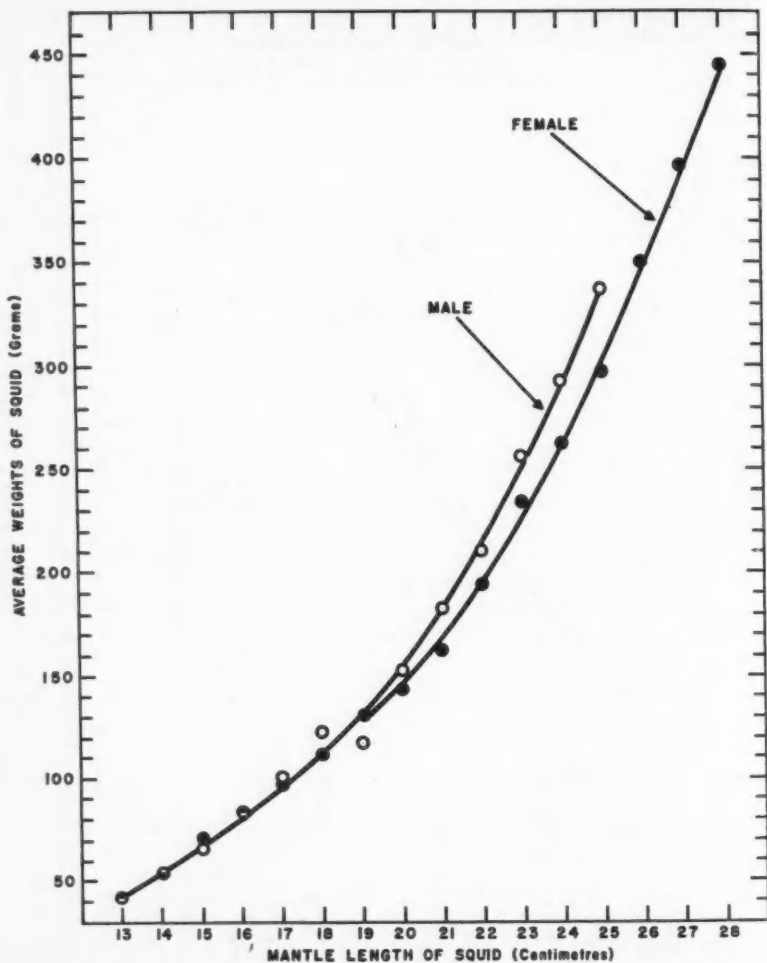


FIG. 11.—Average weights of male and female *Illex* at various mantle lengths, 1952.

RATIO OF FIN LENGTH TO MANTLE LENGTH

The length of the fin, relative to mantle length, was similar in males and females. As the squid became larger and older the ratio of fin length to mantle length became greater: about 35% at 12 cm. mantle length and about 40% at 24 cm. (Fig. 12). An increase in ratio of fin length to mantle length with increase in size occurs also in *Loligo pealii* (Verrill, 1881).

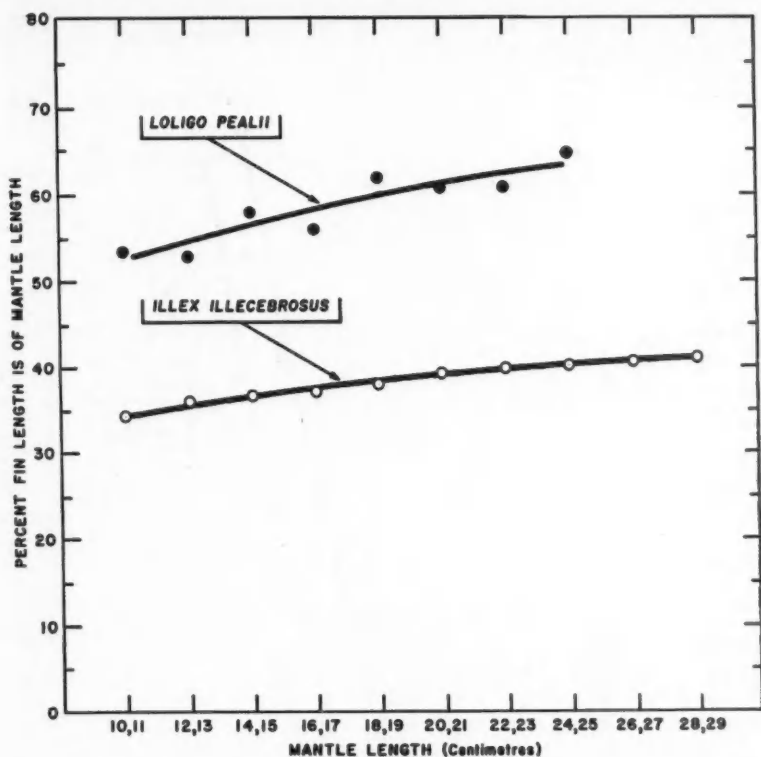


FIG. 12.—Fin length as a percentage of mantle length in *Illex* and *Loligo*. (Data for *Loligo pealii* from Verrill, 1881, pp. 324–332.)

SEXUAL MATURITY

MALES

In the monthly catches, up to August the volume of the testis of the male squids was less than 1 cc. (less than 1% of body weight), in all but a few large individuals (Fig. 13). The testis was measured by displacement of water in a 10 cc. graduated cylinder. In Fig. 13 weight of the testis is calculated from volume, given 1 cc. = 1.1 g.: a conversion factor arrived at by weighing and measuring volumes of 20 testes. November values are calculated from body weights of squid in September and October, except in squid of mantle lengths 16 and 18 cm. when these values are calculated from weights in May to August. Even in larger squid (up to 23 cm. maximum mantle length) spermatophores were not present in the spermaries, and hectocotylization with loss of suction discs occurred in only a few up to the end of August. In the late season, however, development toward maturity was accelerated. Testis volume increased to more than 4.0 cc. in the majority of squids, i.e., more than 1% of body weight, and a

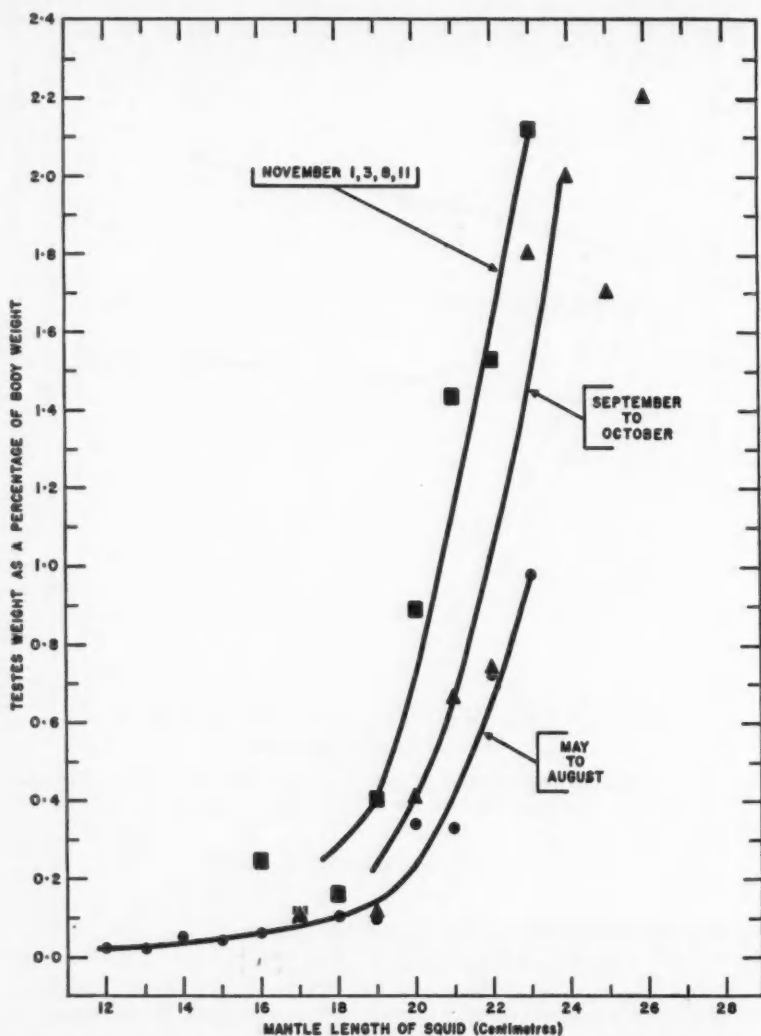


FIG. 13.—Maturity of male *Illex*. I. Weight of the testis as a percentage of body weight, May to November, 1952. (The sight curves are drawn with attention to the number of measurements of individuals supporting each point plotted.)

considerable number (about 75%) showed early or late development of spermatophores (Fig. 14). Also, as mantle length increased, hectocotylization became more evident, with loss of suction discs sometimes on one side only of the right or left ventral arms, and varying in length from 1.0 to 2.0 cm. of the arm, distally (Fig. 15). The apparent deviation from the 50-50 incidence of right or left arm hectocotylized in squid which occurred at 21 cm. (Fig. 15) is unaccountable:

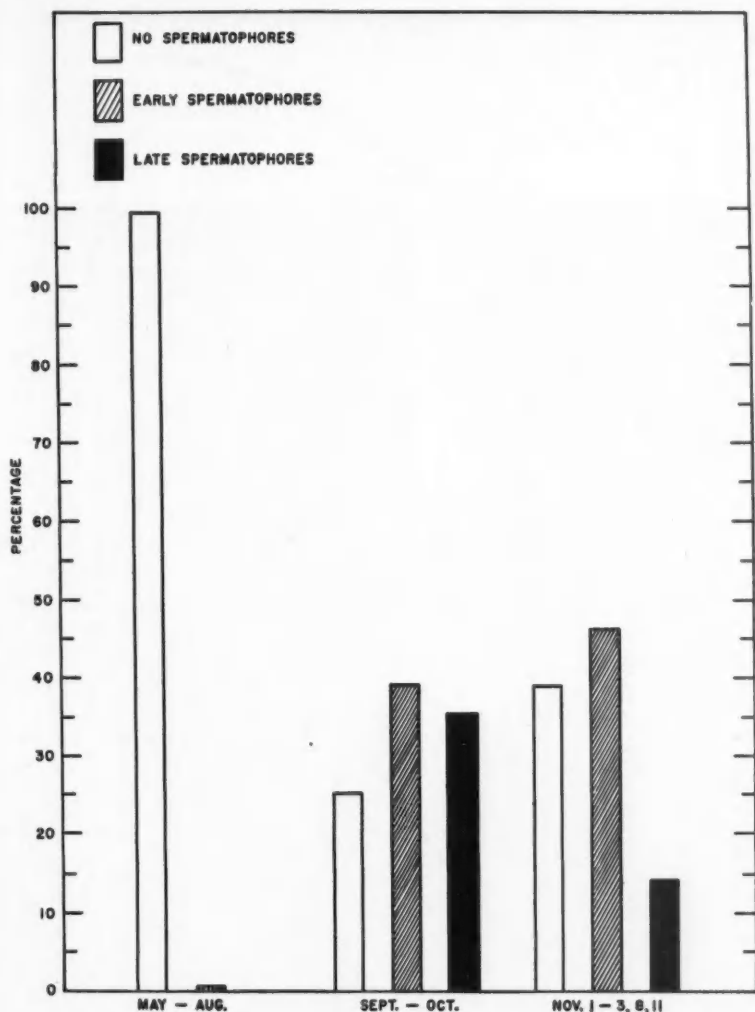


FIG. 14.—Maturity of male *Illex*. II. Spermatophore development, May to November, 1946 to 1952. (Numbers examined for spermatophores: May to August, 229; September to October, 163; November, 28.)

18 squids were examined at this length, and all had the right arm hectocotylized. Hectocotylization was first observed when squids became 20 cm. in mantle length; at this size and over male squids were heavier for their size than females.

Among the mixed group of small and large squids in November, 1952, the smallest males were immature with a testis volume of less than 1.0 cc., 0.1 to 0.4% of body weight, while the largest males were maturing and had a testis

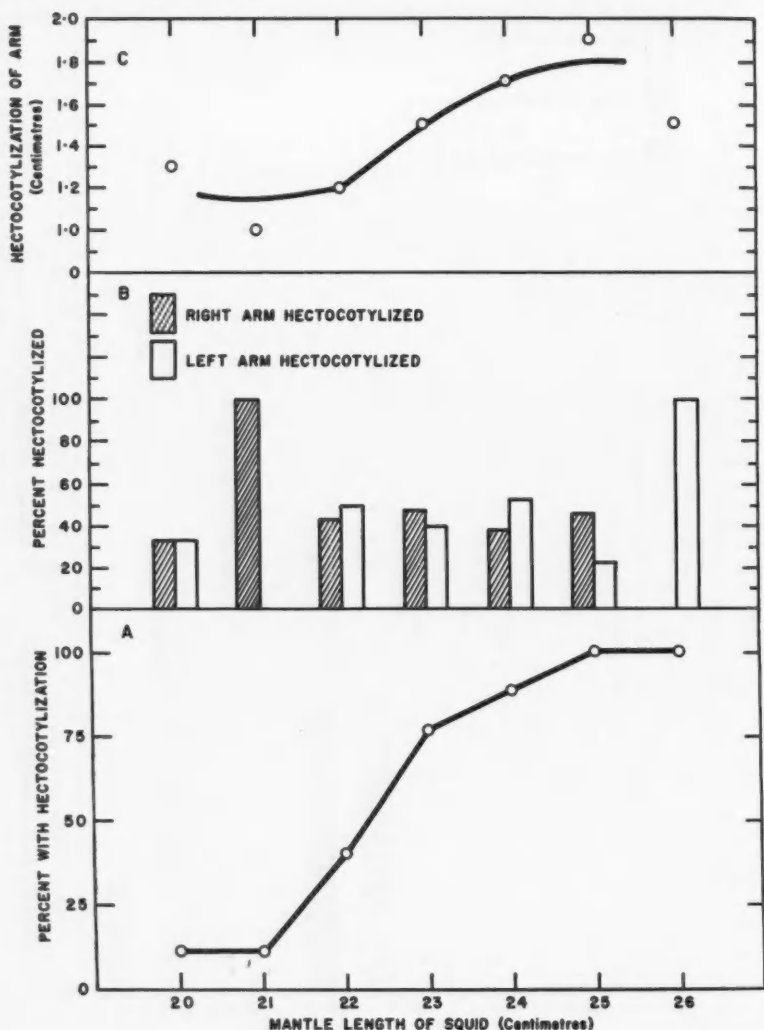


FIG. 15.—Maturity of male *Illex*. III. Hectocotylyzation, 1946 to 1952. A: percentage hectocotylyzation; B: percentage of total with right or left arm hectocotylyzation; C: extent of arm hectocotylyzation, in centimetres. (Number of individuals examined for hectocotylyzation at mantle lengths 20 to 26 cm., respectively, were: 27, 18, 40, 68, 53, 13, 3.)

volume of up to 5.0 cc., and over 1% body weight. However, throughout the season the volume of the testis and the weight of the testis relative to the body weight increased, also, for squid of a given length; showing the overall influence of season on maturity (Tinbergen and Verwey, 1945). In the inshore area, only a

few of the larger males taken had spermatophores ready for transferral, so that maturity of most males must come some time later and presumably in the deep water. In the mature male captured in May, 1953, the spermatophores were fully developed and many were extending from the penis to the siphon through which undoubtedly some had been released (Fig. 16).

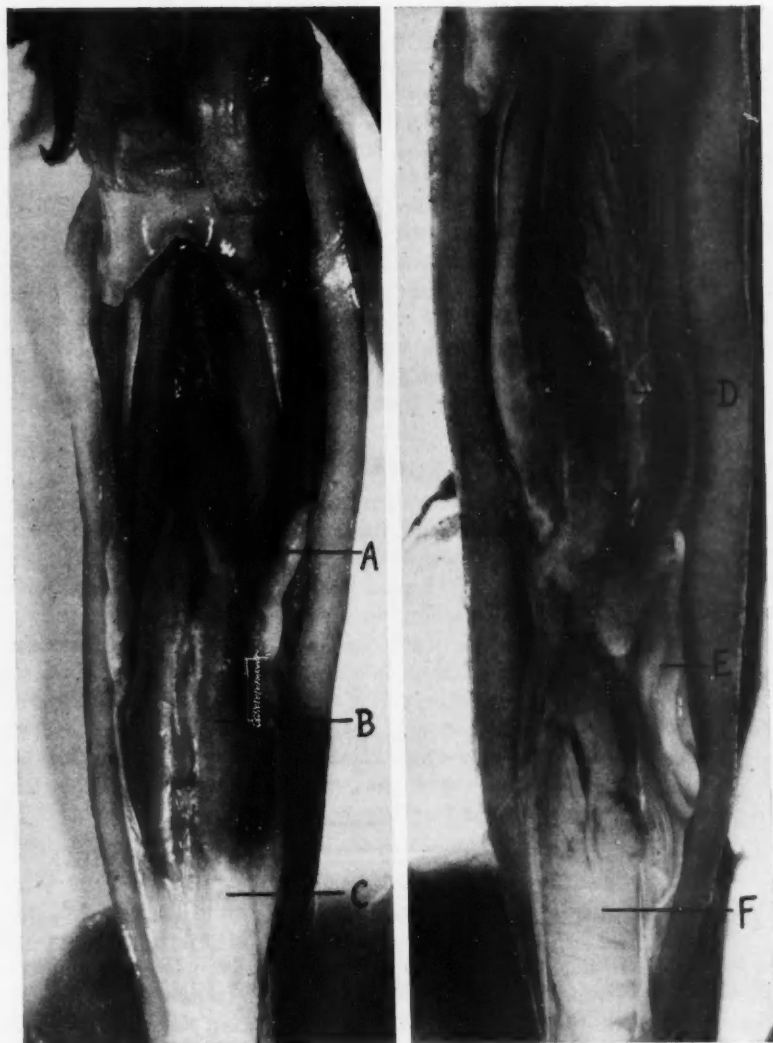


FIG. 16.—Photograph of maturing female and mature male *Illex*, May, 1953. A, oviduct; B, nidamental gland; C, ovary; D, spermatophores; E, spermary; F, testis.

FEMALES

Measurements of long diameters of the largest eggs of squid were made throughout the season in 1951 and 1952, using an ocular micrometer and at 30 \times magnification. From May to November as the squid became larger (Fig. 17), the eggs increased gradually in size from a diameter of 0.1 mm. to 0.3 mm.,

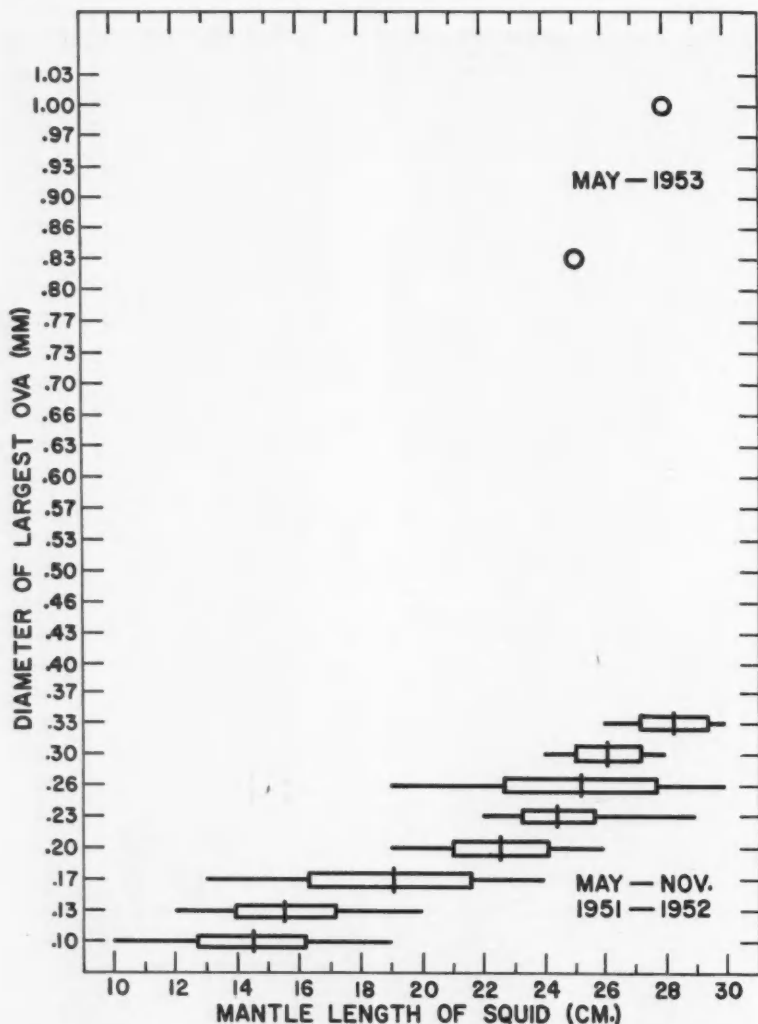


FIG. 17.—Graph of egg diameters of *Illex*, 1951 and 1952, and May, 1953. Average mantle length (vertical lines), standard deviation $\times 2$ (rectangles) and range of mantle length at each egg size (horizontal lines).

and did not exhibit the sharp rise in the rate of development which seemed to have occurred in the male sexual products in September and October. A few anomalies in the size of eggs were found but these only in the mixed group of November, 1952. For example, on that occasion a squid of 19 cm. mantle length had an egg diameter of 0.26 mm., which in a squid of the same mantle length would have been 0.17 mm., at the most, in the early season.

An unusual capture was made on the Grand Bank in March, 1952, of a female with eggs of 0.3 mm.; this stage of maturity, therefore, approximated that of females taken inshore in late autumn. Also, in 1953, squid were taken in January and February on the Grand Bank which were about as mature and approximately the same size as squid taken inshore in November (Table VII). In May, 1953, two large maturing females, taken on the Grand Bank by the *Investigator II*, had egg diameters of 0.83 and 1.00 mm., larger than any reported heretofore for this species (Fig. 17). Mature eggs of *Loligo pealii* are 1.5 to 1.6 mm. in greatest diameter (Williams, 1909). In most females in our samples the nidamental glands were whitish and thin; they were about 3 cm. long in squids of 26 cm. mantle length in November. However, the nidamental glands of the large squids (28 cm. mantle length) taken in May were 7.6 cm. long, orange in colour and quite thick, a probable indication that *Illex* does provide a gelatinous matrix to enclose the eggs when they are laid. The egg mass was pale yellowish. These large female squids would probably have spawned in the summer following capture.

FOOD

Frost and Thompson (1933) reported squids feeding mostly on crustaceans, even near the coast in 1932, but generally found no food in stomachs of squids in their 1931 inshore samples. Our samples examined for stomach contents were from the Grand Bank and inshore, at different times in the year, 1946 to 1952, and altogether comprised about 1,500 specimens. The food in the stomachs was in a macerated condition, much as described by Verrill (1881). Occasionally the food was almost completely digested and structureless except for melanophores, which were presumably from fish. D. E. Sergeant (personal communication) observed at Dildo, July 21, 1954, that a squid ate a capelin it had captured, starting at the head and biting it into small pieces which were swallowed until the capelin was completely devoured. Inshore surface plankton, largely copepods, was found in only a small percentage of stomachs of squid taken inshore (Table IX).

STOMACH CONTENTS

About 750 each of male and female squids in random samples, 1946 to 1952, were examined for stomach contents.

Small squids were taken on the outer edge of the Grand Bank where they were feeding mostly on euphausiids (Fig. 18). The comparatively high percentage of stomachs with fish at 13 to 18 cm. (Table IX) is misleading because the stomach contents often had euphausiids as well and in greater quantity than fish remains. There was little or no difference in feeding between the sexes at these

TABLE IX. Stomach contents of *Illex*, 1946 to 1952. Percentage of stomachs with food, which had the species indicated present. Some stomachs had more than one species.

Mantle length in cm.	10-12	13-15	16-18	19-21	22-24	25-27	28-30
	%	%	%	%	%	%	%
Species:							
Capelin	...	5.9	9.3	16.5	4.7	1.4	...
Redfish	5.9	15.9	5.4	6.9	2.7	2.8	12.5
Gadoid (cod & haddock)	...	1.5	9.3	...	4.1	2.8	...
Fish fragments (unidentifiable)	5.9	13.9	18.2	27.4	46.6	55.6	50.0
Total fish	11.8	37.3	42.2	50.7	58.2	62.5	62.5
Euphausiids	52.9	48.3	69.3	21.9	4.1	1.4	...
Amphipods	11.8	5.0	1.1	2.7	8.1	4.2	...
Mysids	1.4	3.4
Copepods	...	1.5	0.4	1.4	...
Shrimp	...	2.0	1.1	1.4	6.1	1.4	...
Crustacean fragments	11.8	7.5	3.6	12.3	10.1	1.4	...
Squid	5.9	8.0	3.2	2.7	4.7	16.7	25.0
Pteropods	5.9	...	2.1	...	1.4
Whelks	...	1.5	2.1
Polychaetes	...	0.5	...	1.4	2.7	1.4	...
Chaetognaths	1.8	1.4
Total invertebrates	88.2	74.3	84.3	43.8	37.8	26.4	25.0
Amorphous material (partly digested)	5.9	10.4	2.5	5.5	14.2	12.5	25.0
No. of squids examined	67	364	336	181	381	158	16
No. with food	17	201	280	73	148	72	8
Empty (% of total squid)	74.6	44.8	16.7	59.7	61.1	54.5	50.0

small sizes. Among large squids, however, fewer females (44%) than males (50%) had empty stomachs; but this small difference may not be significant.

Larger squids taken inshore were feeding mostly on capelin and other fishes (Fig. 18). Generally, no invertebrates were found with fish in stomachs of large squid. Fish fragments included:

Capelin (*Mallotus villosus*) (eggs, vertebrae, scales and otoliths),

Redfish (*Sebastes marinus*) (scales and bones),

Cod (*Gadus callarias*) (scales, vertebrae, otoliths),

Haddock (*Melanogrammus aeglefinus*) (scales) and

Mailed sculpin (*Triglops pingeli*) (hypurals and otoliths).

There was some evidence of feeding on small flounders as well. Scales, otoliths, vertebrae, bones and eggs were used to identify the fish. Many fish fragments were not referable to species.

The percentage of total females feeding on invertebrates was 35% while that of the total males was 32%. This small difference was partly due to large female squids feeding on other squids. Pelagic invertebrates taken were chiefly euphausiids. These were in fragments in the stomachs and could not be referred definitely to species. *Thysanoessa* sp., and *Meganyctiphanes* sp. would appear to be the principal genera involved. A pelagic shrimp, *Pasiphaea* sp., was taken in 3 stomachs only. Only a few semi-benthonic forms like shrimp (*Pandalus montagui* Leach, observed in one), gammarid amphipods, small gastropods and polychaetes were in evidence.

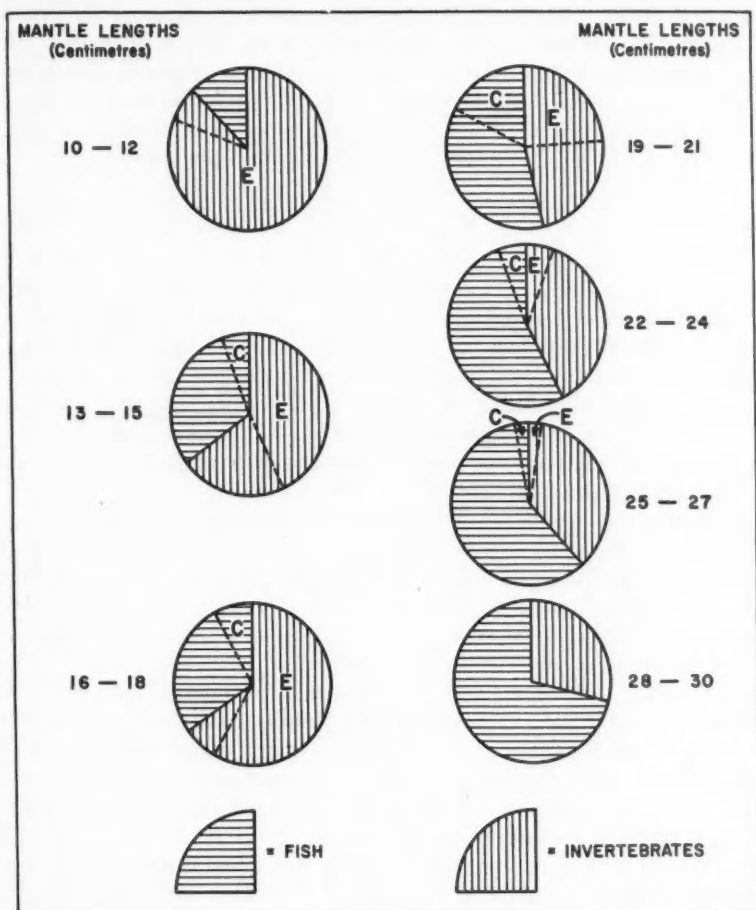


FIG. 18.—Percentage of stomachs of *Illex* with food (Table IX) which contained fish and invertebrates, 1946 to 1952; also, percentage of stomachs with capelin—C, and euphausiids—E.

PARASITES

The squids examined were parasitized by larval tapeworms and occasionally larval nematodes. Plerocercoids of *Phyllobothrium* sp. were found free in the stomach, caecum and rectum; and plerocercoids of *Dinobothrium* (*sensu lato*) sp., encapsulated in the walls of the caecum and rectum.

Phyllobothrium sp. Dollfus has been reported in the stomach of *Loligo loligo* at Arcachon, France, and in the stomach of *Todaropsis eblanae* at Concarneau, France. *Phyllobothrium dorni* Oerley was reported in *Todarodes* (*Ommatos-*

trephes) *sagittatus* at Naples and *Dinobothrium plicatum* Linton in the intestinal wall of *Illex illecebrosus* at Princetown (*sic*), Mass., U.S.A., (Dollfus, 1936). Miss N. Frost (in unpublished notes without description) reported tapeworms in *Illex illecebrosus* at Bay Bulls in 1931. The present author noticed plerocercoids similar to *Phyllobothrium* sp. in *Loligo pealii* supplied to students at McGill University by the Woods Hole Marine Biological Laboratory in 1953.

PHYLLOBOTHRIUM SP.

These plerocercoids were mostly large, about 20 mm. long (when fully extended about 50 mm.); and when living moved freely between the stomach, caecum and rectum of the squid. Sometimes they came out at the anus, and were seen in considerable numbers on the surface of landed squids. In the squids examined, usually only a few parasites were found in the caecum of each, but occasionally many were found in a squid. This plerocercoid was sensitive to touch: when touched it invaginated its scolex and contracted itself (Fig. 19, C, D). When relaxed, the scolex was extended and the four sessile bothridia with anterior accessory sucker were clearly seen (Fig. 19, A, B).

Infestation was greater in the small squids (average length about 17 cm.) arriving on the banks early in the season (Fig. 20). Since these plerocercoids may escape freely from the squid it would appear that they did so after reaching a certain stage in development.

The final host may be infected by this plerocercoid when it escapes from *Illex*, which, however, may be a true intermediate host. The plerocercoids of *Phyllobothrium* sp. were quite active in sea water, swimming or crawling over a substrate at fair speed with contracting and expanding movements, and exploring with mobile bothridia. They were killed by a slight rise in temperature. The most completely relaxed specimens, however, were dead when taken in the morning from the surface of squids landed overnight. The final host for this genus is reported to be skates, rays and sharks (Joyeux and Baer, 1936). The primary host, conceivably a crustacean which may feed incidentally on faecal material from skates, would pick up eggs of the tapeworm and harbour the proceroid. Tetraphyllid larvae have been reported in *Calanus* sp. by Marshall and Orr (1955).

DINOBOOTHRIUM (SENSU LATO) SP.

The plerocercoids of this species were encapsulated in the walls of the caecum and rectum, but mostly in the spiral part of the caecum. They were small: not more than 2 mm. long. They were motile in the capsules in live specimens examined, and with scolices evaginated (Fig. 19, E); but invagination of the scolex was common and occasionally all were found in this condition (Fig. 19, F-H).

Unlike the plerocercoids of *Phyllobothrium*, infestation with *Dinobothrium* was low in the early season—less than 30% in squid of mantle lengths up to 18 cm.

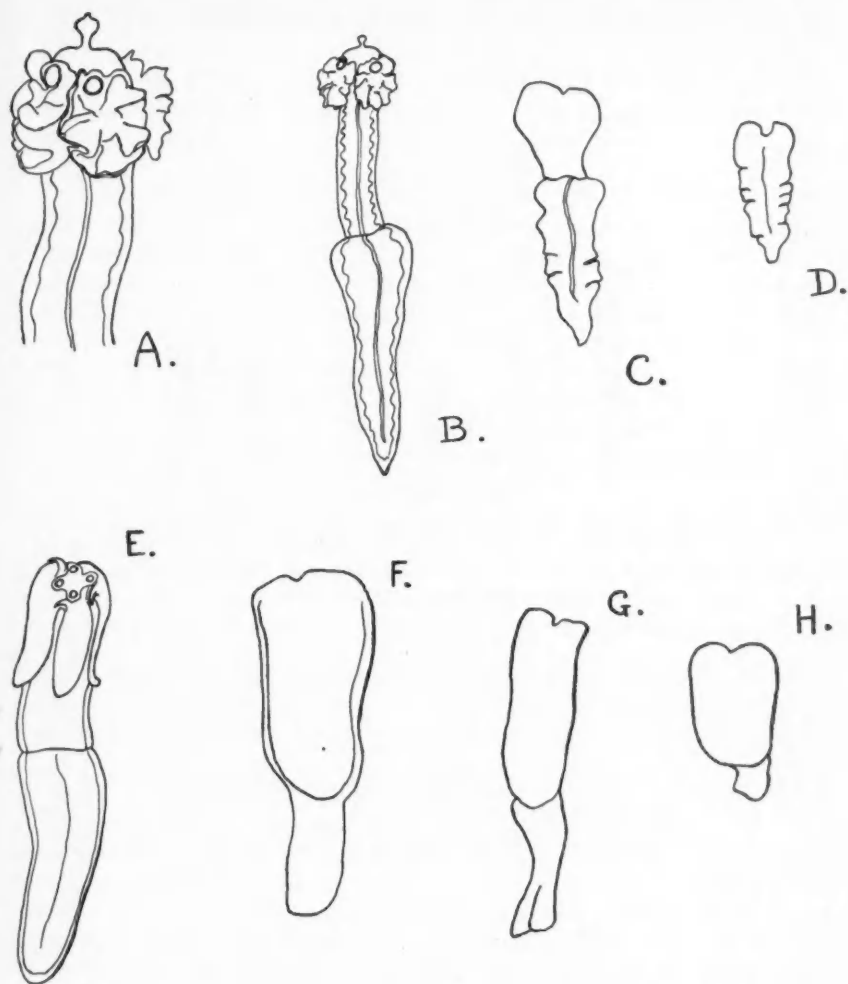


FIG. 19.—Cestode plerocercoids infesting *Illex*: *Phyllobothrium* sp., A–D; *Dinobothrium* (*sensu lato*) sp., E–H. B = about 20 mm. in length; E = about 1.5 mm. in length.

—but rose in the late season to about 80% at mantle lengths of 22 to 30 cm. (Fig. 20). It would appear, therefore, that the main source of infestation is on the Grand Bank where the squid feed heavily on euphausiids, which may be a primary host for this tapeworm. However, we have not examined euphausiids for the proceroids.

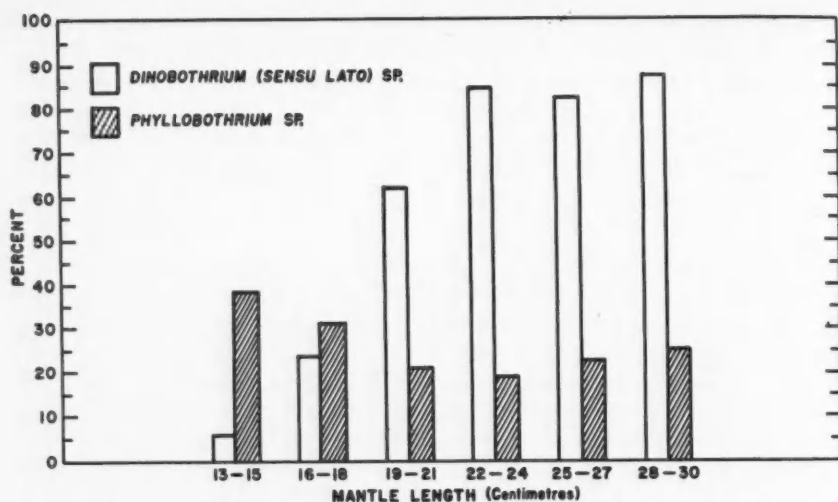


FIG. 20.—Percentage of *Illex* parasitized with plerocercoids of *Phyllobothrium* sp. and *Dinobothrium (sensu lato)* sp., May to November, 1952. Total squids examined at each length group from 13–15 to 28–30 cm. were, respectively, 106, 166, 137, 264, 103, 8. Some squids were infested by both species.

NEMATODES

About 1,500 squids were examined for nematodes. Only 1.3% were infested with one larval nematode each, embedded in the walls of the stomach and caecum or free in the body cavity. Most of these larval nematodes were very small and were not identified.

The incidence of nematodes appeared to be higher in the larger sizes of squid (Table X); and this might be expected, because the squid at these sizes in the inshore area are feeding on small fish, such as capelin, which are often infested with nematodes.

TABLE X. Nematode larvae in *Illex illecebrosus*.

Length of mantle	Number examined	Percentage infected
cm.		%
10–15	431	0
16–20	452	1.1
21–25	538	1.9
26–30	82	6.1
Total	1,503	1.3

Nematodes were found in three instances only in the stomachs with food, and in one of these the large nematode (*Porrocaecum* sp.) had been bitten into three pieces. It would appear, however, that although some large nematodes are destroyed when eaten by squid, some might be transmitted intact to a predator incidentally as part of the stomach contents of squid. One of the chief consumers

of squids in the Newfoundland area, the pilot whale, is infested with several species of nematodes, some of which are found in capelin (D. E. Sergeant, personal communication; Templeman, 1948). The squid, however, is not as efficient an intermediate host for nematodes as it would appear to be for fish tapeworms.

ILLEX AND ONE OF ITS CHIEF PREDATORS, THE PILOT WHALE

The short-finned squid, *Illex illecebrosus* (LeSueur), a predominantly oceanic species (Bigelow, 1926), is present in relatively large numbers in the Newfoundland fishing area from late spring until late autumn. Such a large aggregation of a species invites predation, and where the aggregations occur regularly there may arise a critical dependence of the predator on the prey. Should an unprecedented scarcity of the prey species occur, its effect on a predator with specialized feeding habits can be devastating. The pilot whale, *Globicephala melana* Traill, is apparently such a predator. Only rarely has the pilot whale been found to feed on anything but squid (D. E. Sergeant, personal communication), and mostly it is on *Illex*, because the supply of arctic squid, *Gonatus fabricii* (Fabricius), is probably not enough to provide food for the many large herds of pilot whales for very long. In the evolution of such a specialized predator many species of squid may have played a part, but at present during at least six months of the year the many herds of pilot whales in the Newfoundland area subsist on *Illex*. The pilot whale is able to keep in touch with its prey even during the winter, presumably, and it does not migrate inshore except in pursuit of squids. Years of scarcity of squid in Newfoundland, therefore, are marked by a scarcity of pilot whales also, and these animals presumably can only be found where the squid are. It is doubtful whether pilot whale calves can sound deeply (D. E. Sergeant, personal communication). It is likely, however, that when the squid remain far offshore in summer they are schooling near the surface. Schools of squid near the surface have been seen in August on the Grand Bank by the *Investigator II* and by weather ships stationed south of the banks. But during the spawning migration it is presumed that adult squids are at considerable depths. It is not known whether young *Illex*, when past the larval stage, would form pelagic schools which would be under predation by pilot whales on their wintering grounds. Large pelagic schools of young squid, comprising the bulk of the squid which migrate to the Newfoundland area in summer, may move southward before turning north and westward. The extent of their migration into this area, therefore, may be influenced sometimes by the extent of their southward wanderings and the acclimation to higher temperatures than prevail in the Newfoundland area. This may account for their scarcity in these waters in some years.

SUMMARY

1. Squid were taken mostly on the outer edges of the Grand Bank in the early season, March to July. The numbers taken there in any year is an index of relative abundance inshore in the late season, August to November. Migration

into the area appeared to be from the southern edge of the banks northward and westward, reaching as far north as Hebron Hr., Labrador (in our records), and into the St. Lawrence estuary as far as Trois Pistoles (Frost and Thompson's records). Schools of squid are reported at sea in the Newfoundland area and they are reported to be oceanic as far south as the Gulf of Mexico and Cuba.

2. Records of relative annual abundance of squids inshore show no cyclical regularity and may not indicate population fluctuations in the real sense. First arrivals of squid have been earlier in recent years so that a correlation with climatic conditions may exist. During so-called years of scarcity inshore, squid may be present in fair abundance near some parts of the coast, and presumably offshore.

3. Samples of squid from several areas at a given time showed similar modal lengths indicating a single overall population, but a group of small squid in 1952 arrived late in the season. These had mantle lengths similar to early spring arrivals.

4. Length and weight increase from May to September was large but regular, and a low increase in October appeared to indicate that maximum size inshore was reached in October. Average length of mantle was almost doubled in the season and increase in average weight was to almost 6 times the initial size.

5. Males and females differed in weight late in the season; females reached a greater maximum length and weight, but males were heavier than females at the same mantle length.

6. Ratio of fin length to mantle length was 35 to 41% in *Illex* as opposed to 53 to 63% in *Loligo*.

7. Males showed a sharp increase in the rate of development of sexual products in the late season to a condition where copulation would be possible. Females captured inshore did not show a similar condition of maturity: in the late season, eggs measured only 0.3 mm. in diameter. Mature males and late maturing females were taken for the first time in May, 1953. Eggs were 1.0 mm. in diameter and the nidamental glands of the larger female—28 cm. mantle length—were 7.6 cm. long. Spermatophores were ready for transferral, but maturity in the males was not much more advanced than in late October.

8. The stomach contents of about 1,500 specimens were examined. At small sizes when the squid were feeding on the banks offshore, euphausiid crustaceans were taken mostly; more fish were taken at larger sizes when the squid were on the inshore grounds. Fish taken were mostly capelin (*Mallotus villosus*).

9. Squid parasites found were plerocercoids of *Phyllobothrium* sp. free in the stomach, caecum and rectum; and *Dinobothrium* (*sensu lato*) sp. encapsulated in the walls of the caecum and rectum, averaging 52% and 25% infestation respectively. Larval nematodes were present in the body cavity or encysted in the walls of the stomach and caecum in only 1% of 1,500 squids.

10. The pilot whale, which appears to feed almost exclusively on *Illex* in the Newfoundland area, is considered to follow these squid in their migrations,

and when seen south of the Grand Bank may be feeding on pelagic schools of squid. Scarcity of squids in the inshore area in some years might be occasioned by the extent to which these pelagic schools of squid become acclimated to warmer waters in their southward wanderings.

ACKNOWLEDGMENTS

A great deal of credit is due to the technical staff of the Newfoundland Fisheries Research Station who assisted in the collection of squids, particularly Capt. W. Barbour, master of the *Investigator II*, and Messrs. A. Kelland, C. I. Barbour, E. LeGrow, E. LeMessurier, and F. Spencer, at sea, and Messrs. E. Rowe, W. Blackmore and others who helped to jig squid on the squid-jigging grounds for this study.

Mr. H. R. Mullett drew the graphs and map, and Mr. E. L. Rowe did the photographs for this paper.

Dr. D. E. Sergeant made observations on squid and length measurements at Chapel Arm and Dildo in 1952 and 1953 while working on the pilot whale, and also looked up some references on squid which were difficult for the author to obtain. Mr. A. M. Fleming measured squids at Bonavista and St. John's in the author's absence in 1953 and collected parasites. Sergeant and Fleming also helped with bait depot records.

Many thanks are due to these people and to Dr. W. Templeman, Director of the Station, who placed all collected material on squids at the author's disposal and who critically read the manuscript with helpful suggestions for revision. Mr. E. J. Sandeman also read the manuscript and suggested revisions.

Thanks are due, also, to Dr. R. Ph. Dollfus, Museum National d'Histoire Naturelle, Paris, who confirmed the identification of the plerocercoids of the tapeworm parasites, and to Mr. A. M. Fleming who identified one of the larval nematodes.

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Herring Gulls and Common Terns as Possible Predators of Lobster Larvae¹

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ABSTRACT

Herring gulls (*Larus argentatus*) and common terns (*Sterna hirundo*) were collected in the southern Gulf of St. Lawrence when lobster larvae were abundant. No lobster larvae were found in 36 herring gull stomachs and only one in 15 common tern stomachs.

INTRODUCTION

SINCE 1948 a programme of systematic towing for lobster larvae has been carried out in the Northumberland Strait area between Richibucto, New Brunswick, and Miminegash, Prince Edward Island. Wilder (1953) has shown that larvae are abundant in the surface waters there from mid-June to mid-September but suffer heavy mortalities during their planktonic stages. The herring gull (*Larus argentatus*) and the common tern (*Sterna hirundo*) have been considered as serious predators. Mendall (1934) working in the Gulf of Maine reported "young lobsters" in 15% of the herring gull stomachs and 1.9% of the common tern stomachs he examined. To obtain further information on the extent to which these species feed on lobster larvae, specimens were collected under permit issued by the Canadian Wildlife Service.

METHODS AND MATERIALS

From August 13 to September 13, 1956, while towing for lobster larvae, Captain L. I. Cross assisted by J. O. Allain collected 36 herring gulls, 15 common terns, 1 greater black-backed gull and 1 ring-billed gull. The birds were shot while flying over the water at all hours from 5 a.m. to 5 p.m. standard time.

A description of the towing programme and the special plankton net is given by Wilder (1953). In 1956 lobster larvae reached peak abundance during the first half of August when 13,001 were caught in 122 half-hour surface tows or an average of 106.6 per tow. From August 13 to September 13, 1956, 10,232 larvae were caught in 200 tows or an average of 51.2 per tow. Although the birds were collected after the peak of larval abundance the larvae were still plentiful in comparison with the Gulf of Maine and adjacent Bay of Fundy area. Herrick (1895) from the results of 6 years of towing in the Gulf of Maine was struck by their scarcity. Wilder (1953 and personal communication) found only 2 larvae in 39 Bay of Fundy tows.

¹Received for publication November 26, 1956.

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STOMACH CONTENTS

HERRING GULL (*Larus argentatus*)

Of the 36 stomachs examined 31 contained food. The various food groups expressed as percentage occurrence were as follows: insects 67.7, crustaceans 35.5, fish 25.8, plant material 19.4, birds 12.9, unidentified material 9.7, squid 6.5 and mammals 3.2. The insect orders expressed as percentage occurrence were Coleoptera 45.1, Diptera 16.1, Hymenoptera 12.9, Lepidoptera 9.7 and unidentified 6.5. One immature, second-year bird contained from 1,500 to 2,000 flying ants, 10 beetles, 9 flies and 2 moths. The crustacean material consisted of shell fragments and a crab's claw. No lobster larvae were found. In one case it was possible to identify the fish remains as those of the Atlantic cod (*Gadus callarias*). The bird material consisted mainly of unidentifiable feathers, bones and egg-shell fragments but the presence of a small foot suggested that a small perching bird had been taken. One stomach contained the remains of a small insectivore (shrew?).

COMMON TERN (*Sterna hirundo*)

Thirteen of the 15 stomachs contained food. The food groups expressed as percentage occurrence were as follows: insects 76.9, fish 69.2, crustaceans 23.1, and annelids 7.7. The insect orders expressed as percentage occurrence were: Coleoptera 30.8, Lepidoptera 23.1, Diptera 15.4, and unidentified 23.1. The only fish species found was the three-spined stickleback (*Gasterosteus aculeatus*). This species is caught in large numbers in the tow net and evidently swims close to the surface. The head of *Nereis* sp. was found in one stomach. This was probably taken from the surface waters as some of the plankton samples contained the pelagic heteronereid form of *Nereis virens*. The crustaceans present were all pelagic forms, an isopod *Idothea baltica*, a megalops larva of a crab and one fourth-stage lobster larva.

OTHER SPECIES

The stomach of the first-year greater black-backed gull (*Larus marinus*) was empty while that of the ring-billed gull (*Larus delawarensis*) contained insects and plant material.

CONCLUSIONS

The rather limited data presented provide no evidence that the herring gull is a predator of lobster larvae in Northumberland Strait where larvae are abundant in the surface waters. The presence of a single fourth-stage larva identifies the common tern as a predator of lobster larvae but suggests that predation is not serious.

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Oceanographic Features of the Canadian Archipelago¹

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ABSTRACT

Oceanographic data collected during the first cruise of H.M.C.S. *Labrador* to the Canadian Arctic in August and September 1954 permit comparisons of the vertical temperature and salinity structures in Baffin Bay, the Canadian Archipelago and the Arctic Ocean. From a comparison of the temperature-salinity characteristics of the waters in the Arctic Ocean (Beaufort Sea) with those in Baffin Bay, it is found that: (a) the surface waters of the Arctic Ocean are much less saline than those in Baffin Bay, but minimum temperatures are the same ($-1.8^{\circ}\text{C}.$), (b) the waters of the upper 200 m. in Baffin Bay are denser than those found at corresponding depths in the Arctic Ocean, (c) below 200 m., Arctic waters are the denser, and below 500 m. they are denser than any waters found in Baffin Bay, and (d) waters found at 250 m. in the Beaufort Sea, at 500 m. in Smith Sound, and at 1250 m. in central Baffin Bay, have identical temperature and salinity characteristics ($-0.3^{\circ}\text{C}.$, 34.4‰).

In addition the data permitted limited investigations into the effect of drifting ice floes on the vertical temperature structure of the water, the origin of the "north water", long-term variations in the oceanographic conditions in Baffin Bay, and dynamic calculations of currents and volume transports of the waters through the channels leading into Baffin Bay.

INTRODUCTION

THE icebreaker H.M.C.S. *Labrador* was commissioned in early July 1954, and sailed later that month from Halifax, N.S., with ten civilian scientists on board. The scientific programme included investigations in the fields of hydrography, oceanography, cosmic rays, terrestrial magnetism, meteorology, also a sea ice survey, all of which were to be carried out principally in the Lancaster Sound-Barrow Strait regions. In addition to the scientific programme, *Labrador* was committed to the resupply of the Royal Canadian Mounted Police Post at Alexandra Fiord.

On completion of the main assignments in Barrow Strait, *Labrador* steamed to the west to meet with the joint Canada-United States Beaufort Sea Expedition which had come in from the Pacific Ocean. Permission was granted for *Labrador* to complete the Northwest Passage and she arrived in Esquimalt, B.C., late in September. Figure 1 shows a general map of the Canadian Archipelago on which the major geographical features are named.

The general scientific programme for the *Labrador* was directed by the Arctic section of the Defence Research Board of Canada, while the oceanographic programme was planned by the Canadian Joint Committee on Oceanography and carried out by scientists from the Fisheries Research Board of Canada, Atlantic Oceanographic Group.

¹Received for publication November 7, 1956.

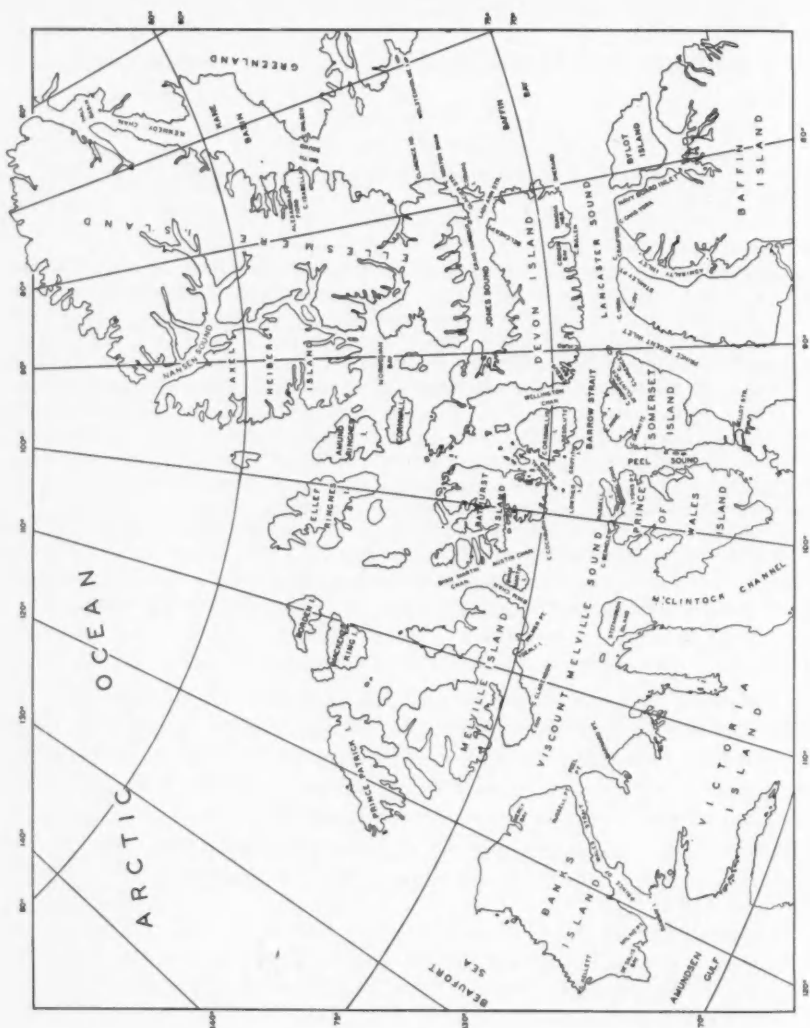


FIG. 1. General map of the Canadian Archipelago.

Some details of a general nature regarding the cruise have been given by Bailey (1955a), and the complete oceanographic details have been presented in mimeographed form (Bailey, 1955b). The data relating to the origin of the deep Baffin Bay water have been analyzed (Bailey, 1956).

PREVIOUS EXPLORATIONS

Smith, Soule and Mosby (1937) and Dunbar (1951) have outlined and commented upon the oceanographic explorations that have been carried out in Northwestern Atlantic and Eastern Arctic waters. Our knowledge of the waters of Arctic America has been built up from the results of a very few oceanographic cruises. The background for the Eastern Arctic is provided through the extensive work in Baffin Bay by the *Godthaab* expedition of 1928, and in the Labrador Sea by the *Marion* and *General Greene* expeditions from 1928-1935.

The principal earlier expeditions which provided basic oceanographic information were the *Sofia* expedition of 1883, from which Dr. A. Hamburg (1884) reported a north-flowing current into Baffin Bay, and the *Tjolfte* expeditions of 1908 and 1909 from which Dr. J. N. Neilsen (1928) combined his own with previous data to describe the three-layer stratification of the waters of Baffin Bay as well as several other features.

The *Godthaab* expedition of 1928 occupied a total of 160 oceanographic stations in Baffin Bay, including the entrances to Smith, Jones and Lancaster Sounds. A large number of observations were also made in Davis Strait and in the Labrador Sea. Considerable detail was provided by the survey which gave not only a good description of the waters, but also indicated the velocities of the various currents and the volumes of water being carried through Baffin Bay (Riis-Carstensen, 1936; Kiilerich, 1939). In the same year the International Ice Patrol commenced a series of oceanographic surveys designed to provide information regarding the drift of ice in the North Atlantic Ocean. During the years 1928-1935, a number of large-scale oceanographic surveys were carried out by United States Coast Guard vessels *Marion* and *General Greene* operated under the auspices of the International Services of Observations and Ice Patrol. The results of these surveys which deal with oceanography, bathymetry, sedimentology and drift of sea ice and icebergs have been presented in Bulletin No. 19 of the U.S. Coast Guard (Ricketts and Trask, 1932; Smith, 1931; Smith *et al.*, 1937).

In the western Arctic large-scale surveys such as the *Godthaab* and *Marion* expeditions have not been undertaken and thus the knowledge of these waters has developed more slowly. Inspector Larsen, R.C.M.P., made observations of surface temperatures and salinity during voyages of *St. Roch* in 1935-37 in the Amundsen Gulf region. These observations have been reported by Tully (1952).

In recent years observations have been made in the Beaufort Sea, Baffin Bay and among the islands of the Canadian Archipelago by ships of various United States Task Groups and by joint Canada-United States expeditions. Some of these data from the western Arctic have been used by Cameron (1953) in studying the oceanography of the Beaufort Sea and Amundsen Gulf.

Several publications have appeared recently which deal with the oceanography of areas adjacent to the Canadian Archipelago. Among these, the oceanographic observations of Project Skijump I and Skijump II in the Polar Sea (Worthington, 1953), the account of the Soviet expedition to the central Arctic in 1954 (Webster, 1954), LaFond's (1954) treatment of the physical oceanography of the seas north of Alaska, and a note on Arctic oceanography and the Lomonosov Range (Metcalf, 1954), are pertinent in gaining an understanding of oceanographic conditions as found in the Canadian Archipelago.

GENERAL PHYSIOGRAPHY

The submerged plateau protruding from the northern coast of North America is described (Canada Year Book, 1954, p. 11) as a major part of the Great Continental or Polar Shelf surrounding the North Polar Sea. On the Polar Shelf lie Iceland, Greenland, all the Arctic Islands of Canada, and most of those of Europe and Asia.

The submarine topography of this continental margin is somewhat hypothetical, but sufficient has been charted to indicate an abrupt break at the northern oceanward edge. This steep continental slope borders the whole western side of the Canadian Archipelago, and constitutes one of the most striking and significant features of the Polar Regions. Deep, well-developed troughs separate some of the islands of the Canadian Archipelago. The deep troughs of Viscount Melville and Lancaster Sounds are separated by a ridge in Barrow Strait, where depths are about 150 m.

Recent charts indicate a sill in Kane Basin with a depth of 250 m. which separates the deep troughs running between Ellesmere Island and Greenland. Soundings at the western end of Jones Sound and in Norwegian Bay are insufficient to reliably determine the depth of the barrier between this area and the Polar Sea. A sill depth of about 150 m. is indicated in the narrow channel between Jones Sound and Norwegian Bay.

The sill depths in the several channels traversing the Canadian Archipelago determine which waters may flow between Baffin Bay and the Polar Sea. Since the temperature and salinity characteristics vary with depth, this matter has considerable oceanographic significance.

GENERAL CIRCULATION

The main inflow to the Arctic Ocean is the Norwegian Current and the main outflow the East Greenland Current. There is also a smaller outflow to the Atlantic through various channels of the Canadian Archipelago.

In Baffin Bay the general circulation is dominated by the northward extension of the warm West Greenland Current which flows along the west coast of Greenland, and the south-flowing cold Baffin Land Current. The Baffin Land Current is formed by contributions from along the length of the West Greenland Current extension and the addition of polar water from the Arctic Ocean which has come through Smith, Jones and Lancaster Sounds.

LOCATIONS OF STATIONS

The area covered during the 1954 cruise (Fig. 2) of H.M.C.S. *Labrador* included Baffin Bay and the channels leading into it, Lancaster Sound, Barrow Strait, Viscount Melville Sound, Prince of Wales Strait and the Beaufort Sea. The locations of oceanographic stations occupied by the *Labrador* are given in the following list and are shown in Fig. 2.

Section	Stations	Occupied (1954)		Locality
I	3-6	August	2	Lancaster Sound
II	9-12	"	4	Lancaster Sound
III	7-8	"	3	Navy Board Inlet
IV	13-14	"	5	Lady Ann Strait
V	15-17	"	6	Jones Sound
VI	18-20	"	6	Glacier Strait
VII	22-25	"	12	Smith Sound
VIII	26-30	"	14	Baffin Bay
IX	37, 39-41	"	16-18	Barrow Strait
X	38, 42-44	"	17-18	Wellington Channel
XI	50-52	"	24	Austin Channel
XII	53-55	"	25	Byam Martin Channel
XIII	56-64	"	26-30	Viscount Melville Sound
XIV	65-67	"	30	Prince of Wales Strait
XV	71-73	"	31	Prince of Wales Strait
XVI	74-75	"	31	Prince of Wales Strait
XVII	80-83	September	6	Prince of Wales Strait
XVIII	85-92	"	12-13	Beaufort Sea

THE WATERS OF THE CANADIAN ARCHIPELAGO

WATER MASSES

The waters of the Canadian Archipelago situated as they are between the regimes of the Arctic Ocean and Baffin Bay are subjected in varying degrees to influences from the two areas. Since the general water movement is from north to south, the influence from the Arctic may be expected to be much the greater.

A description of the waters in the Arctic Ocean has shown that it is composed of three different water types. According to Sverdrup, Johnson and Fleming (1942, p. 658), these are:

1. Arctic surface water exhibiting low temperatures and low salinities.
2. Atlantic water with temperatures between 3 and 4°C. and salinities of 35.1‰. This water has its origin in the Norwegian Sea.
3. Arctic deep water with a characteristic temperature of -0.85°C. and salinity of 34.93‰. This water type has its origin in the Norwegian Sea as pointed out by Nansen (1902) and Sverdrup (1933).

In Baffin Bay the waters are formed from a mixture of three distinct water types which have temperature and salinity characteristics which are in many ways similar to those found in the Arctic Ocean. These are:

1. Surface water exhibiting wide ranges of temperatures and salinities (Riis-Carstensen, 1936).
2. Labrador Sea intermediate water with temperatures greater than 3°C. and salinity of 34.9‰ (Smith *et al.*, 1937).
3. Deep Baffin Bay water exhibiting temperatures of about -0.5°C. and a salinity of 34.5‰ (Riis-Carstensen, 1936).

At any given location in the archipelago, the water column may not contain waters as described above, but it will have mixtures of the typed waters in varying proportions.

It is convenient to subdivide the surface water as defined above into two layers. One, which is designated as the surface layer, has summer temperatures greater than 0.0°C . and low salinities. The other is called the cold-water layer and has temperatures less than -1.0°C . This treatment of the upper waters is useful when comparisons are made with conditions in an area where an extensive surface layer is formed during the summer months.

The vertical distributions of temperature, salinity and density of the water samples in the Canadian Archipelago are given in Fig. 3 to 24. For purposes of discussion the distribution of properties is treated separately for each layer.

SURFACE LAYER

The thin warmed layer of surface water in the Canadian Archipelago has a very wide range of temperatures and salinities as illustrated in Fig. 3 to 24. Surface temperatures reached a maximum of 5.8°C . in Section VII, and in several areas a warmed surface layer was not developed (Smith Sound, Austin Channel and Byam Martin Channel). The thickness of the surface layer varied widely throughout the area. In Section I (Fig. 3), the surface layer was about 75 m. thick at Station 3 and had a maximum temperature of 2.2°C ., whereas at Station 29 (Fig. 10) the surface temperature was 5.8°C . and the layer was only 20 m. thick.

A general comparison of surface conditions indicates that surface temperatures were higher in the eastern part of the archipelago than in the western and that salinities were lowest in the west and highest in the east.

The surface layer which is under the influence of the greatest number of individual factors (insolation, river discharge, ice coverage, etc.) has a wide range of temperatures and salinities. Indications are that the general differences in the temperature and salinity of the surface layers from one area to another are largely caused by differences in the ice coverage.

The horizontal distribution of salinity at the surface is influenced by the concentration of ice. The ice forms a physical barrier which reduces wind stress, and melting ice increases the stability of the water column.

TABLE I. Surface salinities and ice concentrations at several oceanographic stations in the Canadian Archipelago.

Station	Salinity	Ice concentration
	‰	<i>tenths</i>
62	4.1	10
51	12.9	8
40	30.2	5
23	31.3	6
28	32.3	0

Table I shows surface salinities and ice concentration observed at several stations selected at random from across the archipelago. From the Table it is apparent that during the summer, in heavy ice concentration, surface salinities are low. Probably, at ice concentrations of 5/10ths or less, the presence of ice will lower the surface salinity only by small amounts.

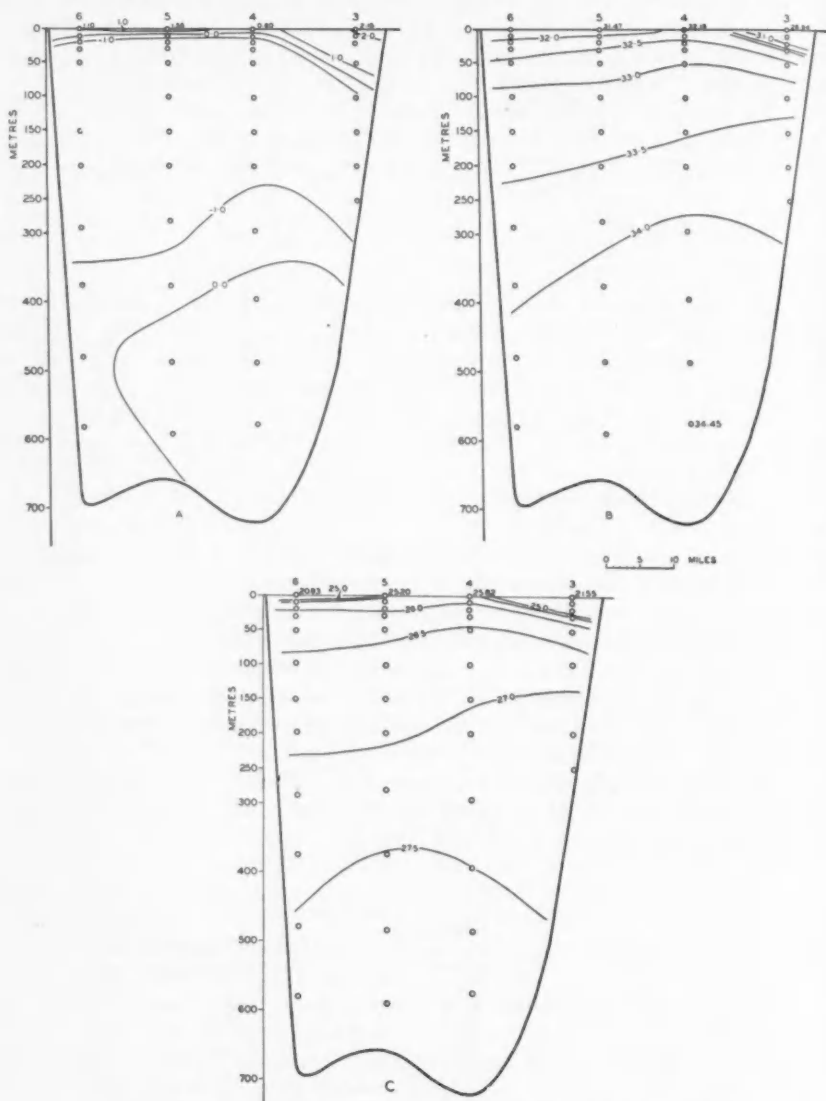


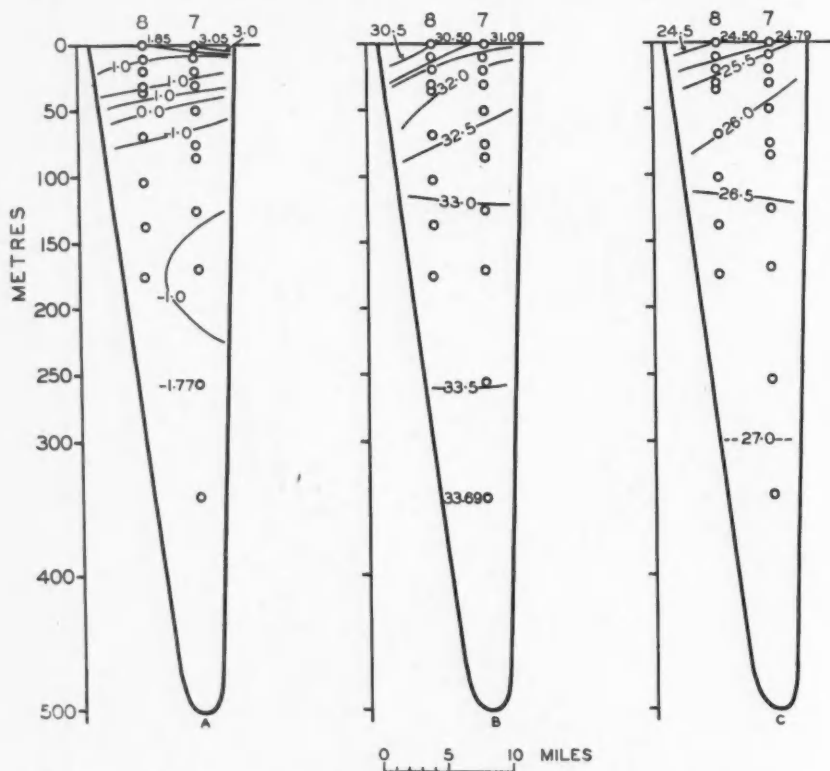
FIG. 3. Distribution of (A) Temperature, (B) Salinity, and (C) Density in Section I.

Salinities in the surface layer were lowest near the shore and in the western part of the archipelago. A maximum of 32.67‰ was observed at Station 18 in Glacier Strait. Surface salinity values higher than 32.0‰ were observed in Wellington Channel and at the entrance to Lancaster Sound. The minimum of 4.1‰ was observed at Station 62 in Viscount Melville Sound.

Several special features regarding the surface layer are discussed under the headings "Some Effects of Sea Ice on Oceanographic Conditions" and "North Water".

COLD-WATER LAYER

The cold-water layer having temperatures less than -1.0°C . was present everywhere throughout the archipelago. It is formed through winter chilling of the surface water (Sverdrup *et al.*, 1942, p. 658). The upper -1.0°C . isotherm was found at depths ranging from the surface in Sections VII and XII to 150 m. in Section IV. However, for most sections it was located at about 30 m. and its depth depended for the most part upon the development of the surface layer.



The lower -1.0°C . isotherm appeared to be closely associated with the 34.0‰ isohaline for stations located in the west and with slightly lower salinities for those in the east. In Lancaster Sound (Fig. 3) the thickness of the cold-water layer was greater than 300 m. whereas in other sections it was generally 200 m. or less. This accumulation of cold water in Lancaster Sound indicates a flow of the lighter cold water from the west towards Baffin Bay. Since the cold-water layer in the Arctic Ocean is lighter than that found in Baffin Bay, the two on meeting will take up positions in the water column relative to their respective densities.

The densities given in Table II clearly indicate that in Lancaster Sound the cold-water layers from the west were superimposed upon those from the east. Section VII (Fig. 9) in Smith Sound also shows the presence of cold water from the Arctic Ocean.

TABLE II. Densities of the cold water layer in several sectors of the archipelago.

Area	Fig. No.	Temperature	Density (σ_t)
		$^{\circ}\text{C}$.	
Beaufort Sea	25	<-1.0	25.0-27.0
Viscount Melville Sound	18	<-1.0	25.5-27.0
Baffin Bay	13	<-1.0	27.0-27.3
Lancaster Sound	5	<-1.0	25.7-27.3

At some depth within the cold-water layer, temperatures reach a minimum. For most sections in the eastern part of the archipelago the minimum occurred between the 100- and 200-m. levels, and had a value of -1.6°C . The lowest observed was -1.77°C . found at Station 7 in Navy Board Inlet (Fig. 5) at a depth of 250 m. In the western area the minimum of -1.77°C . was observed at Station 60 in Viscount Melville Sound at a depth of 75 m.

There were several noteworthy differences between the features of the cold-water layers in different areas of the Arctic. Waters with salinities between 33.0 and 34.5‰ in Viscount Melville Sound were about 0.2 Centigrade degree warmer than those with corresponding salinities found in the Beaufort Sea. However, at a salinity of about 32.4‰, the Viscount Melville waters were about 0.3 Centigrade degree colder. In Lancaster Sound the upper part (50 to 200 m.) of the cold-water layer had temperature and salinity characteristics similar to the waters in the Beaufort Sea at depths of 100 to 170 m. In Smith Sound the upper part (20 to 75 m.) had characteristics similar to the Beaufort Sea and below 75 to about 200 m. it was similar to that found in Viscount Melville Sound between 100 and 200 m. Whether the 0.2 Centigrade degree difference is a significant factor relative to the origin of these waters is problematic.

ATLANTIC WATER

Atlantic water reaches the Canadian Arctic Archipelago from two regions, the Arctic Ocean via the Greenland Sea, and the Labrador Sea via Davis Strait. These waters are relatively warm (3 to 4°C .) and saline (about 35.0‰) as compared with the waters found at lesser depths.

In the Baffin Bay region the Atlantic water reaching the area was specifically named Labrador Sea intermediate water. By the time this water reached the area

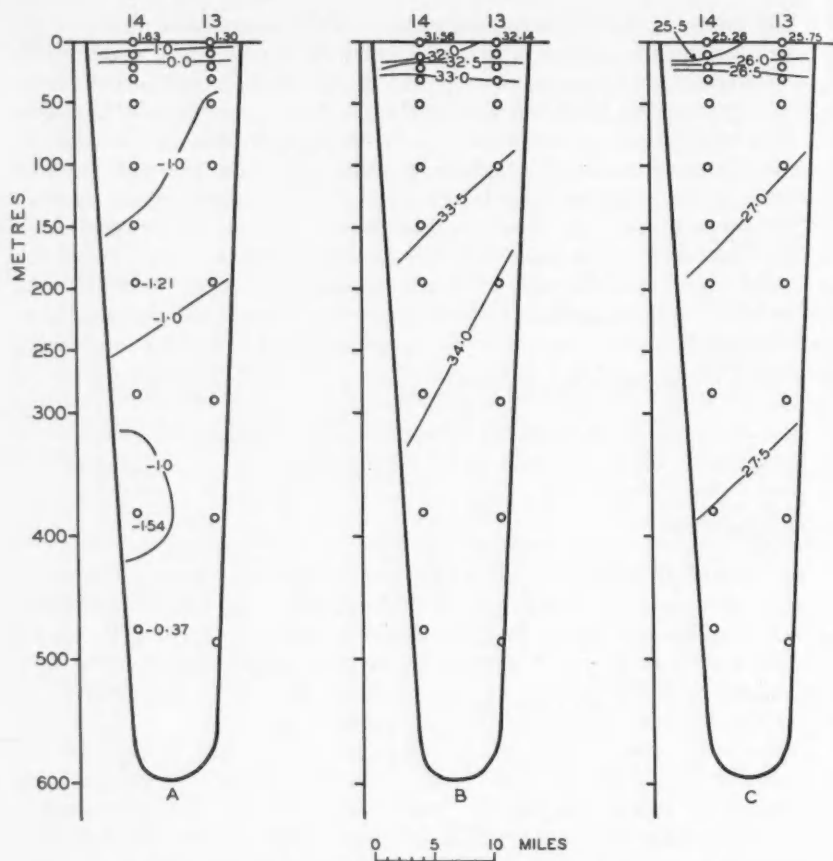


FIG. 6. Distribution of (A) Temperature, (B) Salinity, and (C) Density in Section IV.

of Lancaster Sound it had undergone sufficient mixing with the cold-water layer to have altered its character to a temperature of 1.2°C . and salinity of about 34.3‰. Since the mixing is between two different water masses, any small increase in temperature could be attributed to the presence of Atlantic water. In the western areas, the Atlantic water had undergone more extensive mixing, due in part to its distance from its source, than had Atlantic water found in the eastern areas. Temperatures were lowered to about 0.5°C . with a salinity of 34.8‰.

The thickness of the Atlantic water layer in the eastern areas was at least 300 to 400 m. and constituted the bottom water in the areas investigated. In Baffin Bay this layer had a thickness of about 900 m. as indicated by data given by Riis-Carstensen (1936). In the west it was about 700 m. thick as shown in Fig. 22.

DEEP WATERS

The deep waters which are located below 1,000 m. are not found in the Canadian Archipelago because depths are not sufficient. However, Arctic deep water does approach the area in the west where depths are greater than 1,000 m. Temperatures are less than 0.0°C . and salinities are 34.9‰, as illustrated in Fig. 22 and 23. This water originated in the Norwegian Sea and was formed as a result of winter chilling in which the high salinity surface waters became denser than subsurface waters and replaced them (Nansen, 1902, 1906; Sverdrup, 1933).

In Baffin Bay a deep water is also found below the warm Atlantic waters. Bailey (1956) has demonstrated that the deep Baffin Bay waters were formed in the Arctic Ocean and flowed through Smith Sound. On the basis of temperature-salinity relationships the deep Baffin Bay water was similar to that found at depths of about 200 to 250 m. in the Arctic Ocean and probably originated in

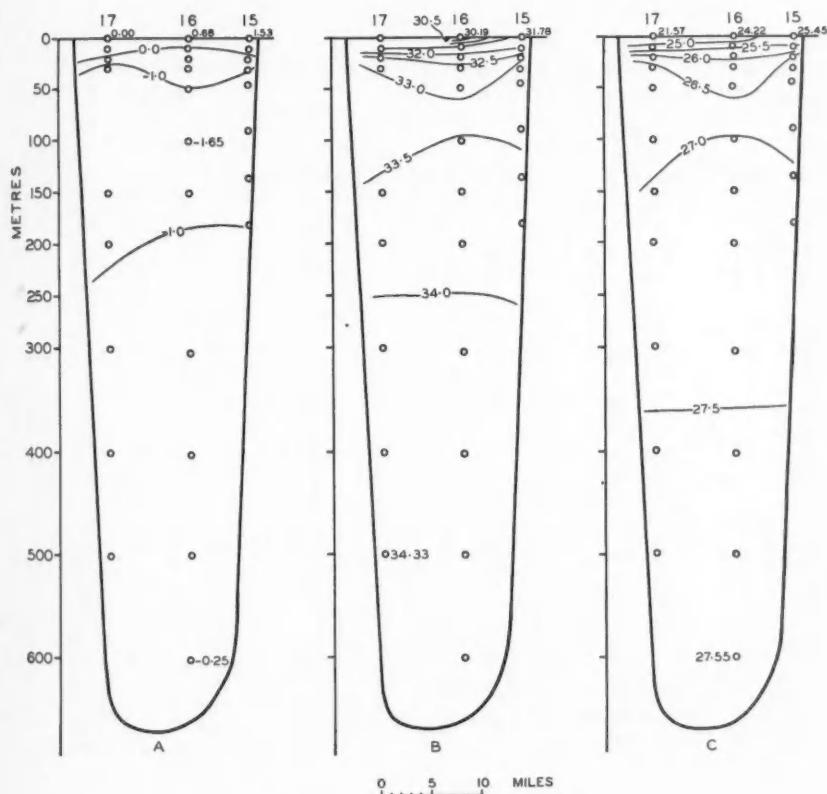


FIG. 7. Distribution of (A) Temperature, (B) Salinity, and (C) Density in Section V.

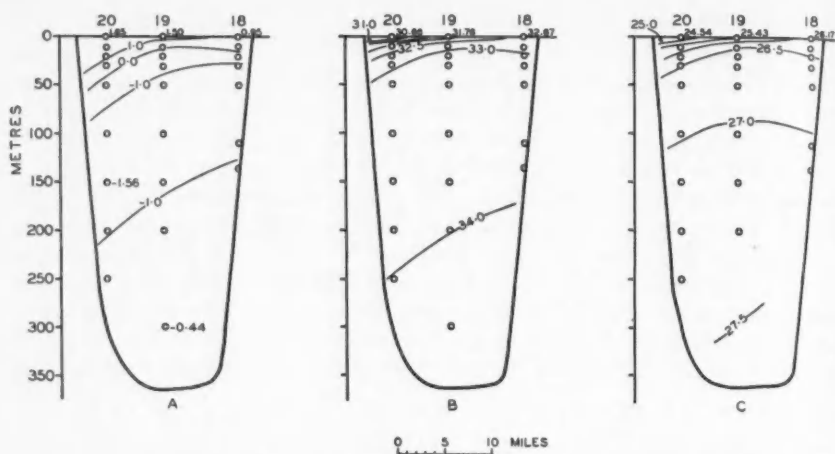


FIG. 8. Distribution of (A) Temperature, (B) Salinity, and (C) Density in Section VI.

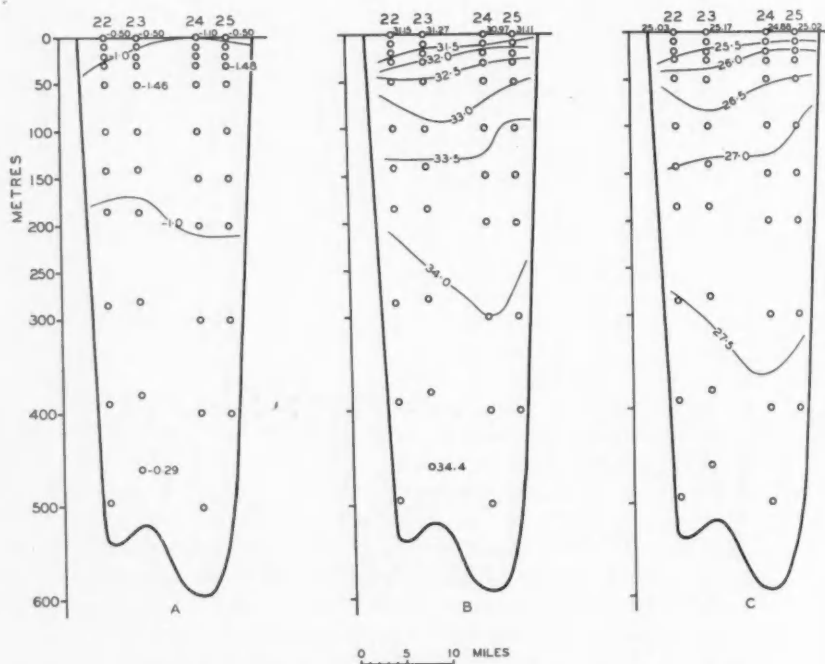


FIG. 9. Distribution of (A) Temperature, (B) Salinity, and (C) Density in Section VII.

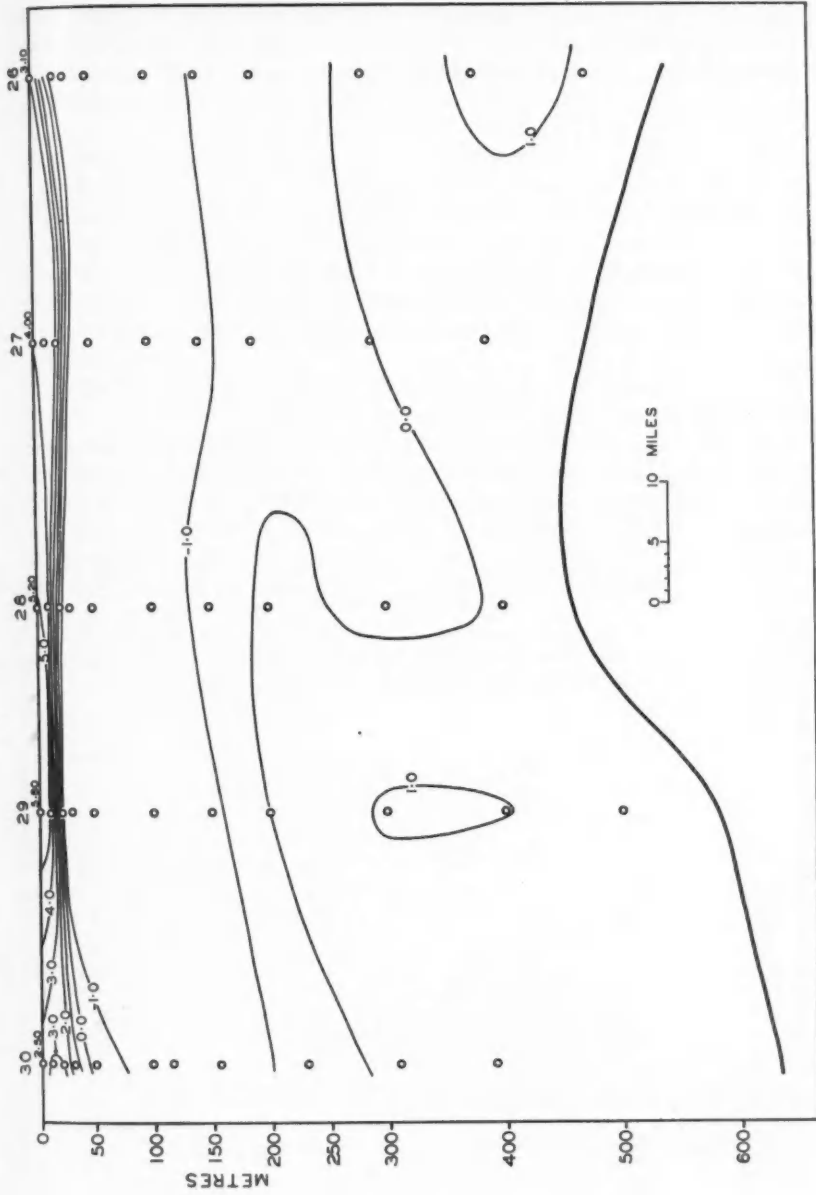


FIG. 10. Distribution of temperature in Section VIII.

that area. Previous ideas held that this water was formed in the wintertime due to cabelling. This is not the case, however, since the cold surface waters do not attain sufficient density to reach depths greater than several hundred metres.

WATER MOVEMENTS

Some indication of water movements can be derived from the vertical distribution of density (σ_t) in section. The slopes of the isopycnals give general indications of relative direction and strength of currents. In Fig. 24, for example, a slope downward from left to right indicates a current into the paper, and vice-versa. The steepness of the slope indicates the strength of movement. The water movements are discussed using this "rule-of-thumb" and the whole is summarized in Fig. 25, which shows the movements of the surface water as derived from the density distribution.

In Lancaster Sound the westward current extended to a depth of 100 m. at Station 3 (Fig. 3) as it flowed along the coast of Devon Island. On the south side an easterly surface current extended to the centre of the sound. Below the surface this eastward current extended across the section between the 100- and 200-m. levels. Below this the eastward flow increased on the south side, but a westerly flow was indicated on the north side.

In Section II (Fig. 4) there was no indication of a continuation of the westward flow indicated on the north side of Section I. Such a flow was

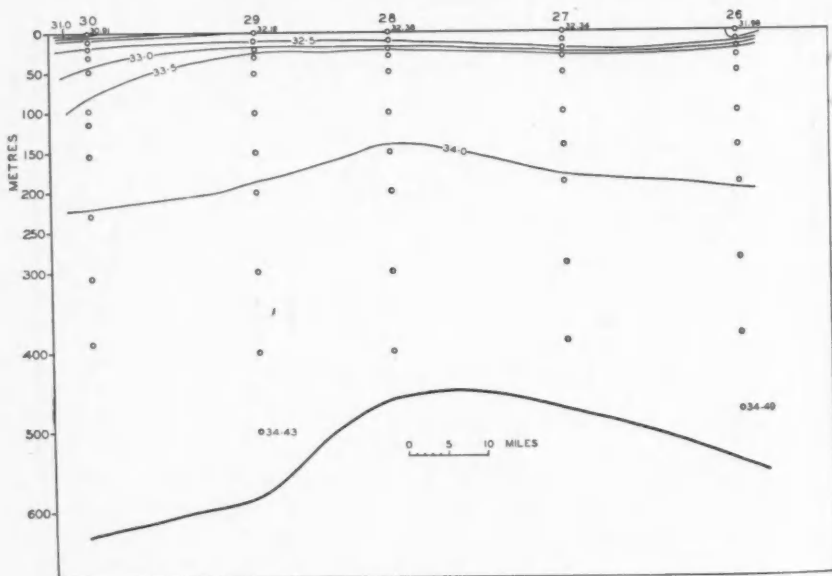


FIG. 11. Distribution of salinity in Section VIII.

confirmed by the drift of icebergs and by the properties observed to the west, and may have been confined to the north of Station 12 in this section.

In the region at the entrance to Jones Sound (Fig. 6, 7, 8) a general westward movement through Glacier Strait and a southward movement through Lady Ann Strait are indicated. In Jones Sound the water movements appeared to be more complex with an eastward flow taking place in the surface layer across the section. The cold water layer, however, moved westward on the north side and eastward on the south side. Movements in the deep waters, although slight, were generally eastward.

In Smith Sound (Fig. 9-C) the slopes of the isopycnals indicate that the waters were moving southward in the upper 200 m. while at greater depths there was a northward movement on the western side and a southward one on the eastern side.

In Baffin Bay (Section VIII, Fig. 12), the density distribution indicated that currents were weak in this area except near the coast where a strong southward flow from the Jones Sound area was in evidence.

It may be expected that the flow through Barrow Strait (Fig. 13-C) would have a considerable influence on water movements in Lancaster Sound because of its direct connection to the Arctic Ocean through Viscount Melville Sound.

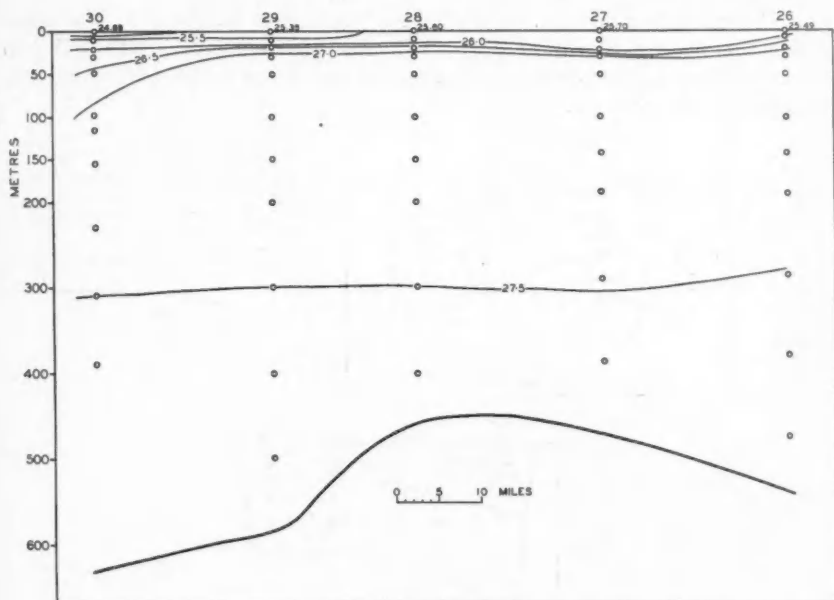


FIG. 12. Distribution of density in Section VIII.

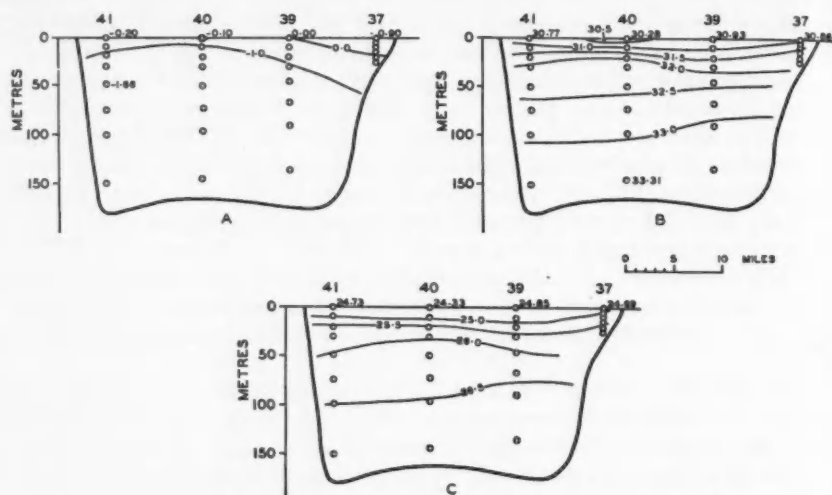


FIG. 13. Distribution of (A) Temperature, (B) Salinity, and (C) Density in Section IX.

This did not appear to be the case, however, since the density distribution gave no indication of any strong flow through the strait at that time.

The movement of water in Wellington Channel as indicated by the distribution of density shown in Fig. 13-C was predominantly southward into Lancaster Sound. The southward flow existed across the entire section and was strongest on the west side.

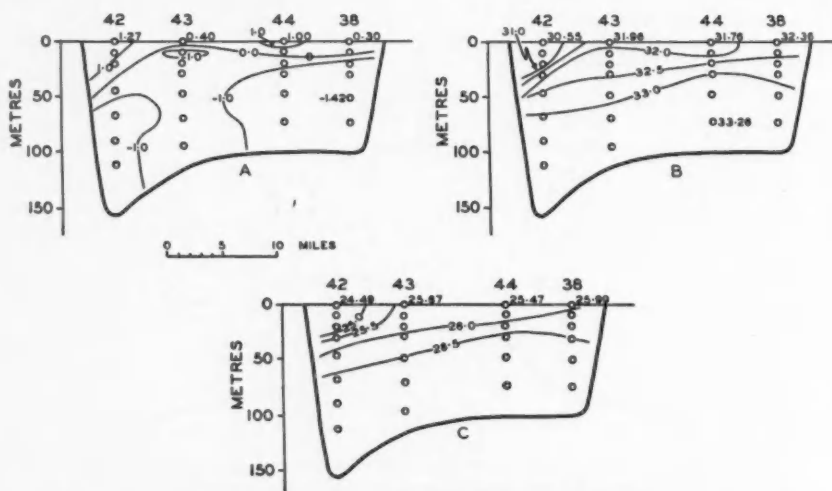


FIG. 14. Distribution of (A) Temperature, (B) Salinity, and (C) Density in Section X.

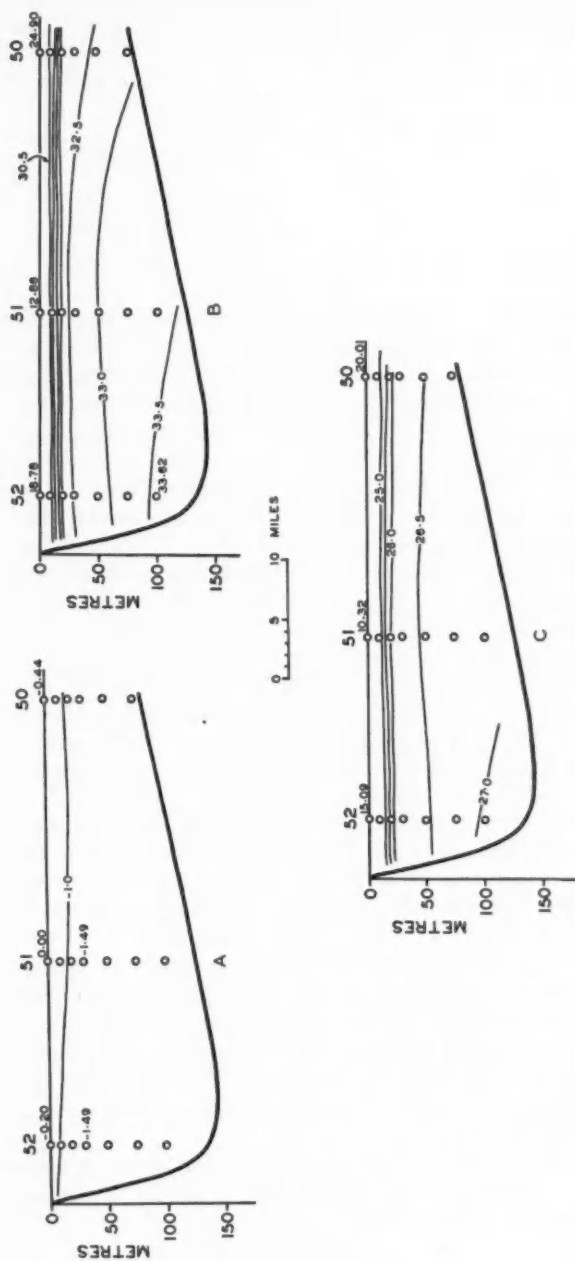


FIG. 15. Distribution of (A) Temperature, (B) Salinity, and (C) Density in Section XI.

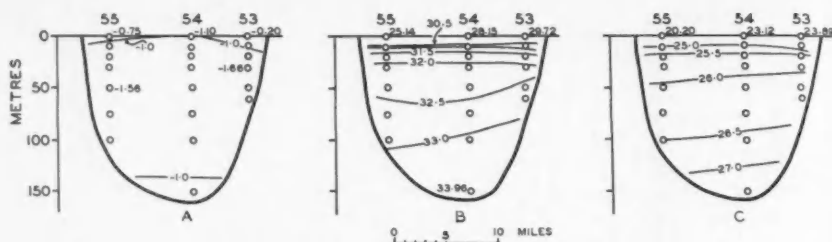


FIG. 16. Distribution of (A) Temperature, (B) Salinity, and (C) Density in Section XII.

On the basis of the indicated movements in Barrow Strait and in Wellington Channel, it would appear that the channel contributes more water from the Arctic Ocean to Lancaster Sound than does the strait. At least this appears to have been so at the time of the observations. The relative strengths of the currents might change radically under a different set of meteorological conditions.

In Austin Channel, Byam Martin Channel and Viscount Melville Sound (Fig. 15-C, 16-C, 17-C) the current were very weak. There was one noteworthy exception to this. In the vicinity of Station 64 an eastward current was observed (visual) which appeared to be about 5 miles wide. The distribution of properties in section has been drawn to indicate this. Further evidence of the narrowness of this current was provided by observations west of the section which showed that the current was continuous with one found flowing northward in Prince of Wales Strait (Fig. 18-C, 19-C, 20-C).

The distribution of density in Section XVIII shown in Fig. 24 indicated that there was a northward movement of warmer waters along the west coast of Banks Island, while along the edge of the continental slope the movement was southward. Between Stations 91 and 92, the water movements were northward.

PRINCE OF WALES STRAIT

In Prince of Wales Strait four cross-sections were made at varying intervals throughout the length of the strait. Three were made in the northern portion while a fourth was located at the southern entrance. The distributions of temperature (A), salinity (B) and density (C) for these sections are given in Fig. 18, 19, 20 and 21.

When *Labrador* arrived at Prince of Wales Strait, it was clear of ice with the exception of a small amount near Russell Point. The vertical temperature distribution at that time indicated a strong northward movement of warm water as shown in Fig. 18. Surface temperatures were greater than 5.0°C . on the east side and as low as -0.6°C . on the west side. The warm water confined to the eastern side of the strait reached to a depth of 50 m. Below this, temperatures were less than -1.0°C .

Salinities were distributed in a manner similar to the temperatures, with the low salinities located on the eastern side. Salinities in the section ranged from less than 24.5‰ to about 32.5‰.

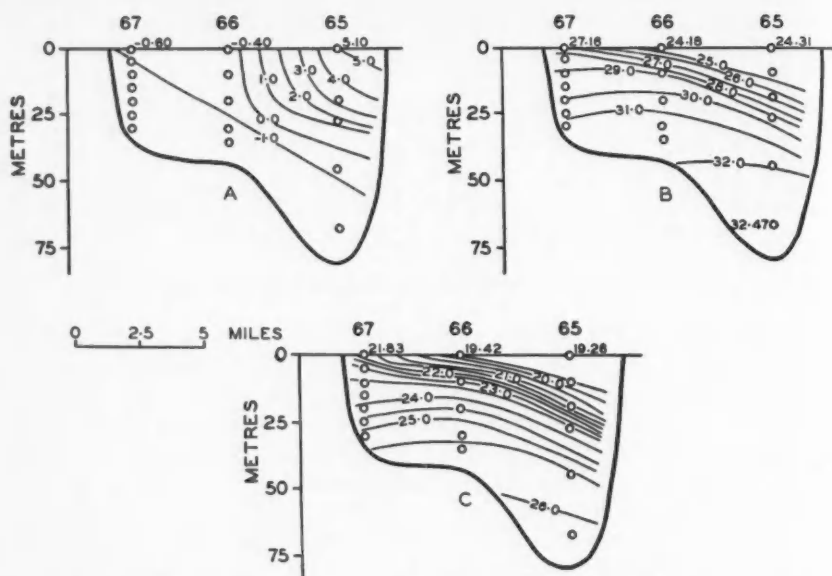


FIG. 18. Distribution of (A) Temperature, (B) Salinity, and (C) Density in Section XIV.

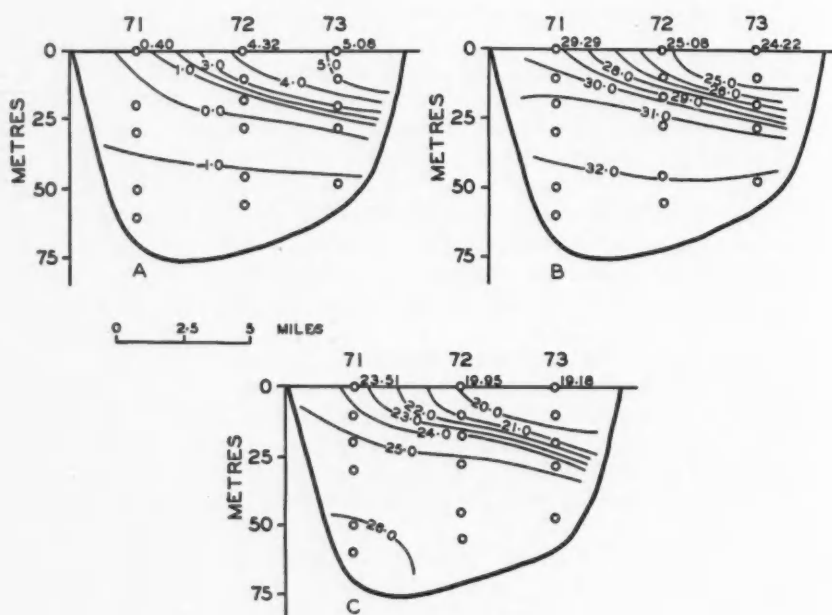


FIG. 19. Distribution of (A) Temperature, (B) Salinity, and (C) Density in Section XV.

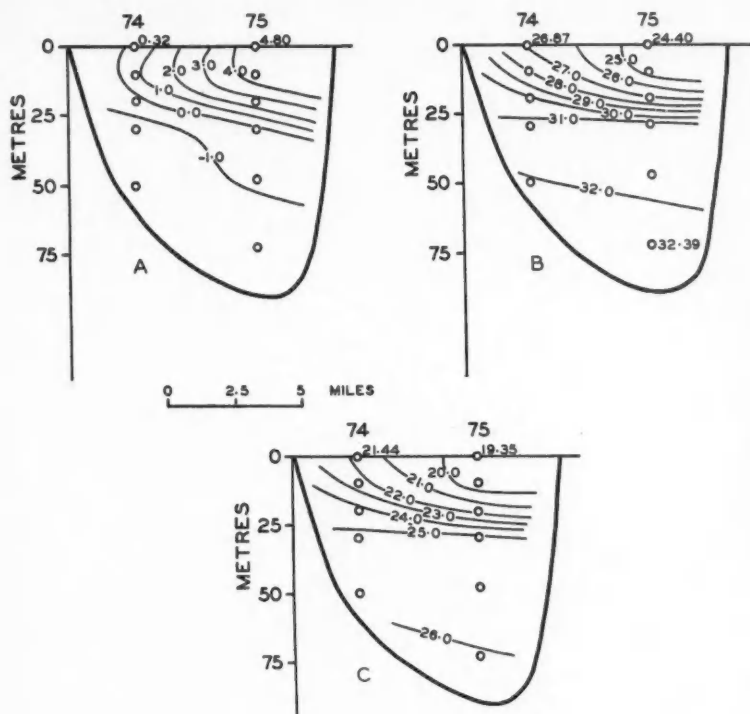


FIG. 20. Distribution of (A) Temperature, (B) Salinity, and (C) Density in Section XVI.

The slopes of the isopycnals give a picture of what was taking place in the strait at that time. The main body of water was moving northward throughout most of the section and a weak counter-current, below 20 m. between Stations 66 and 67, was moving southward into the strait.

Sections XV and XVI showed essentially the same details as were shown by Section XIV.

The southern section across Prince of Wales Strait (Fig. 21) was completed about one week after the northernmost section was made. There was a remarkable contrast between the two sections at the ends of the strait. Whereas the northern section showed a marked tilting of the isopleths, the southern section showed them to be nearly horizontal, particularly in the upper 50 m.

In the upper 30 m., temperatures ranged from $-1.0^{\circ}\text{C}.$ to greater than $5.0^{\circ}\text{C}.$, but below this, waters were almost uniformly cold to the bottom (150 m.). Surface temperatures were all above $5.0^{\circ}\text{C}.$ and a minimum of $-1.58^{\circ}\text{C}.$ occurred at 75 m. Salinities ranged from 24.14‰ at the surface to 32.28‰ at 150 m. at Station 82.

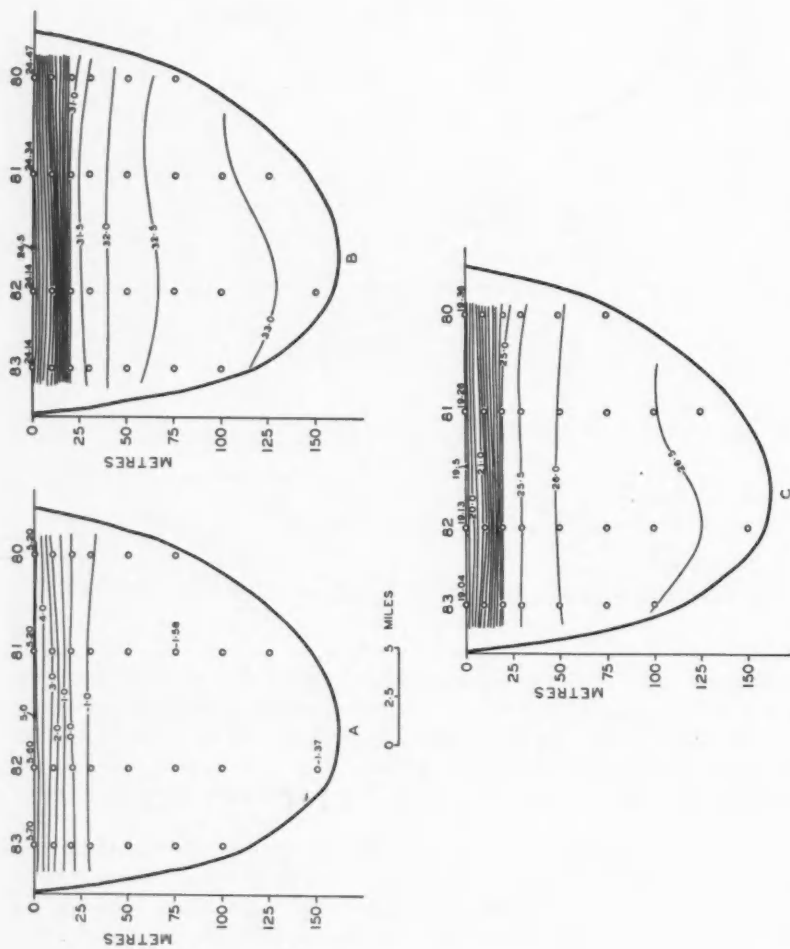


FIG. 21. Distribution of (A) Temperature, (B) Salinity, and (C) Density in Section XVII.

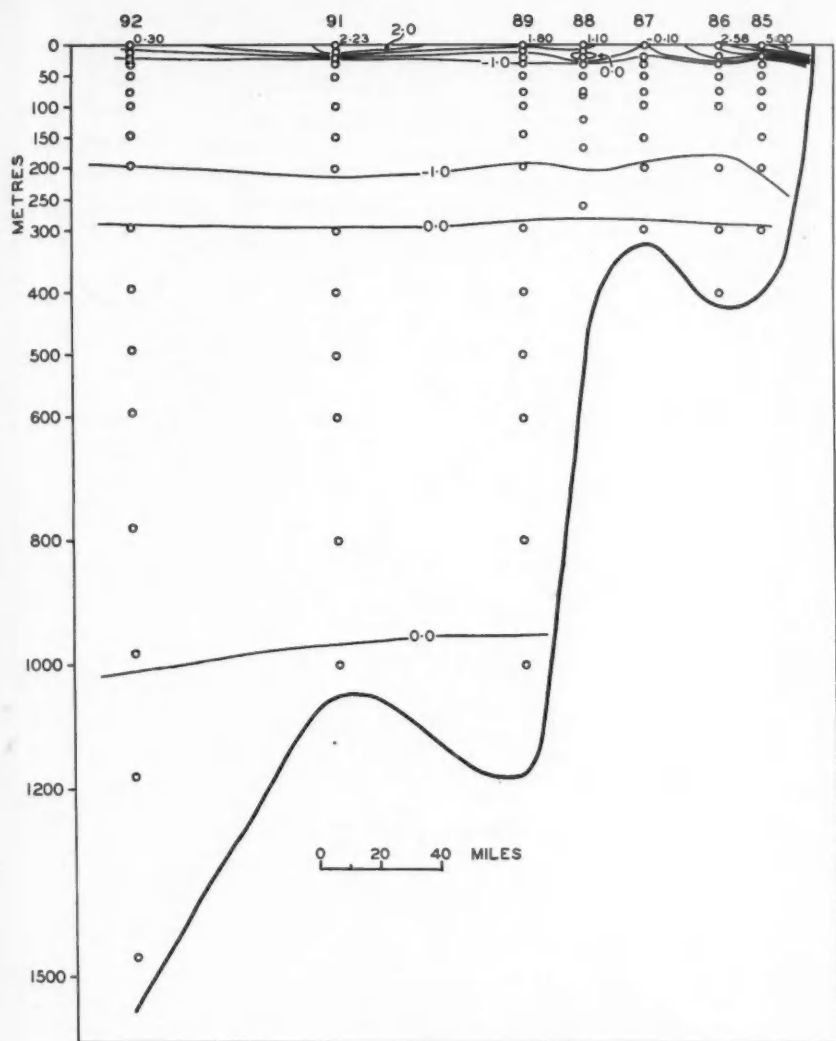


FIG. 22. Distribution of temperature in Section XVIII.

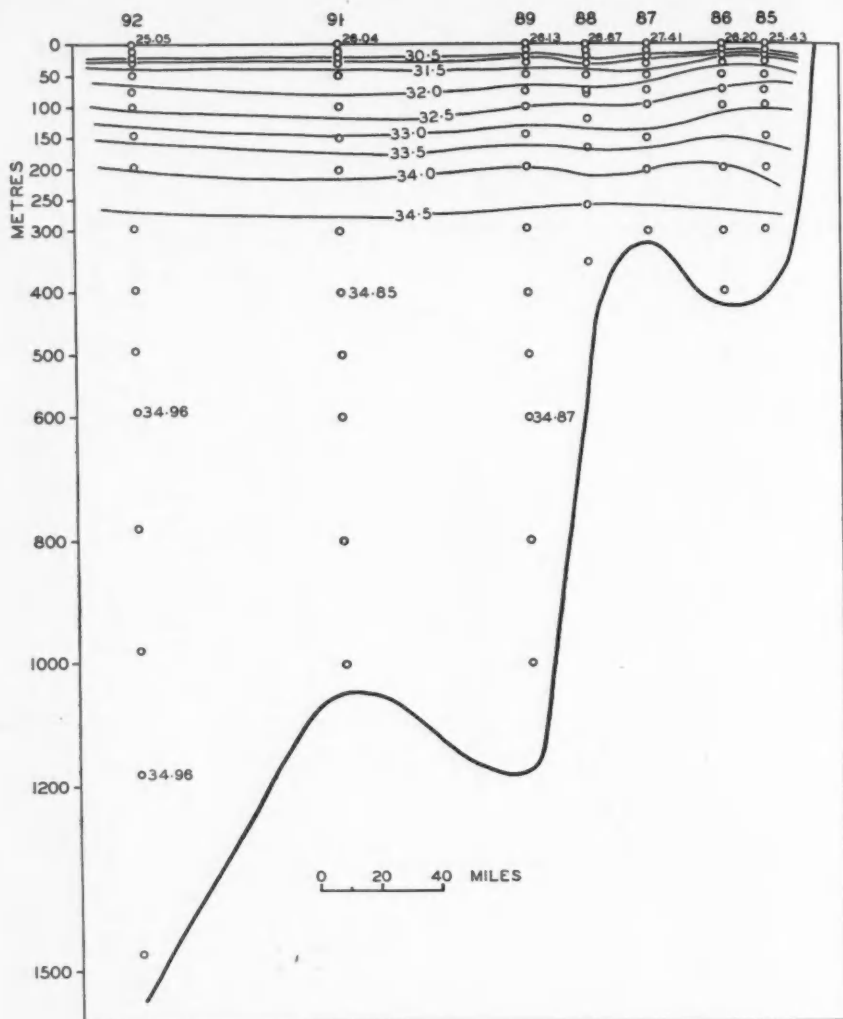


FIG. 23. Distribution of salinity in Section XVIII.

The distribution of density indicates that there was no appreciable movement of water in the upper 50 m. These were the waters which entered into the movement in the northern part of the strait, as discussed above. The cross-sectional area of Section XVII is about three times that of the ones further north, and the currents, if continuous, should be about one-third of those in the north. However, none are indicated. It is conceivable that during the interval between the taking

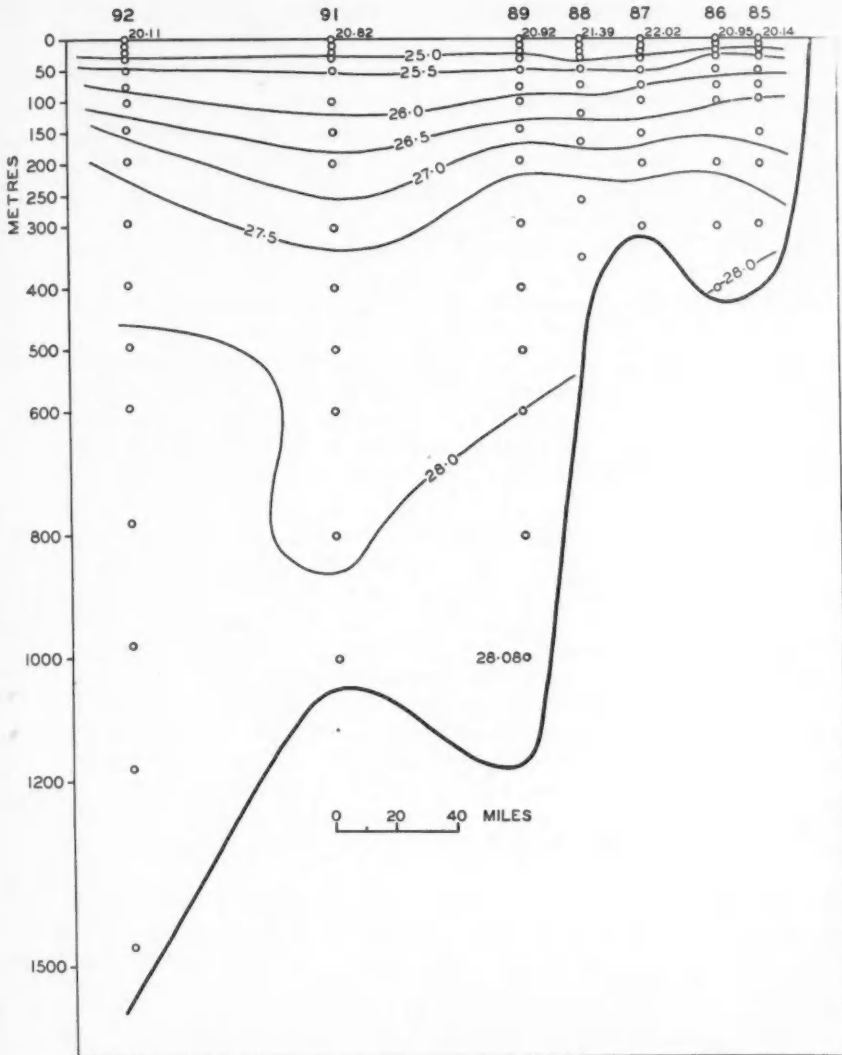


FIG. 24. Distribution of density in Section XVIII.

of Sections XVI and XVII, the dynamics of the system had changed so that transports were markedly reduced, giving only a small flow through the strait. Dynamic calculations showed that the net volume transport through Prince of Wales Strait at Section XIV was of the order of $0.5 \times 10^6 \text{ m}^3/\text{sec}$. The transport through Section XVII in the upper 75 m. was only $1/20\text{th}$ of this value.

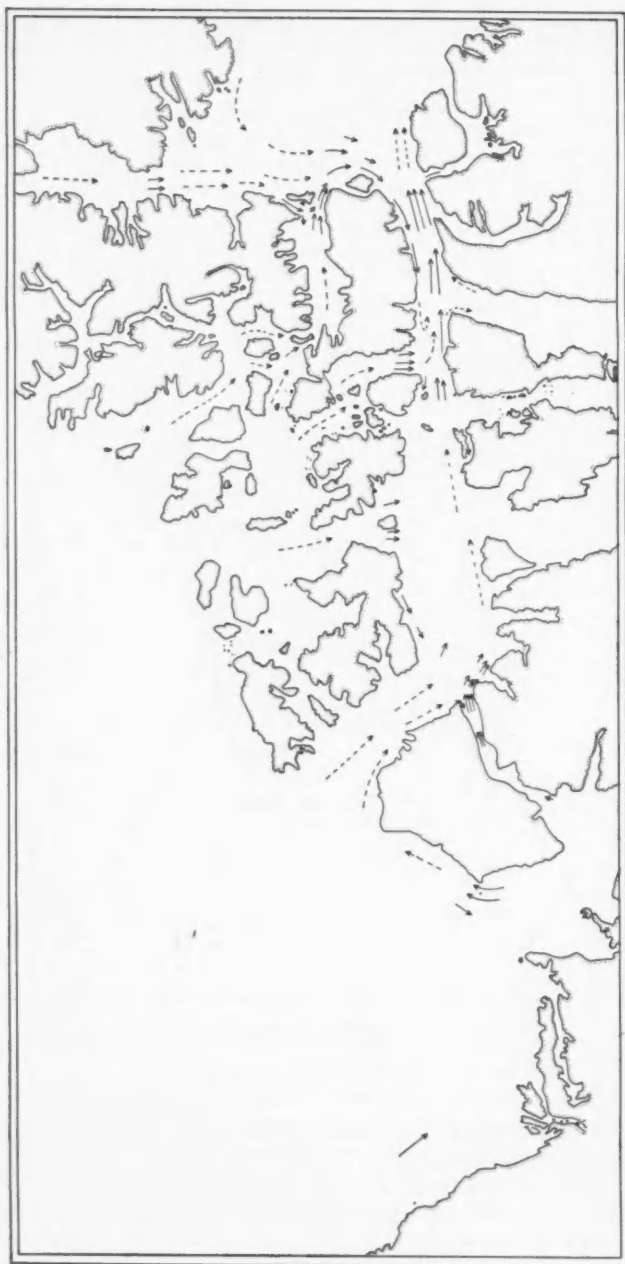


FIG. 25. Water movements in the Canadian Archipelago as derived from the density distribution (→), and as inferred from these movements (---→).

TEMPERATURE-SALINITY (T-S) CORRELATION CURVES

Figure 26 shows typical T-S curves found in the Arctic. Those in the upper diagram are typical of Baffin Bay, Smith Sound, Viscount Melville Sound and the Beaufort Sea. The T-S curve for Station 29 is representative of the waters in the central part of Baffin Bay, which are a mixture of four water types:

1. Surface water with high temperatures and salinities greater than 32.0‰.
2. Cold water with temperatures less than -1.7°C . and salinities of about 33.7‰.
3. Labrador Sea water with temperatures greater than 3°C . and salinity of 34.9‰.
4. Deep Baffin Bay water exhibiting temperatures about -0.5°C . and corresponding salinity of 34.5‰.

At Station 29 only the surface and Arctic waters were found as defined above. The Labrador Sea water that reached Station 29 had undergone a considerable amount of mixing with the Arctic water so that its temperature was slightly less than 1.2°C . and its salinity was 34.3‰. The waters found below this level were a mixture of the Labrador Sea-Arctic water and Deep Baffin Bay water.

The next important T-S curve is that for the Arctic Ocean represented by the curve for Station 89 in the Beaufort Sea.

The waters in the Arctic Ocean are made up of three different water types. According to Sverdrup, Johnson and Fleming (1942, p. 658) these are:

1. Arctic surface water exhibiting low temperatures and low salinities.
2. Atlantic water with temperatures between 3 and 4°C . and salinity of 35.10‰. This water has its origin in the Norwegian Sea.
3. Arctic deep water has a characteristic temperature of -0.85°C . and salinity of 34.93‰. This water type has its origin in the Norwegian Sea as pointed out by Nansen (1902) and Sverdrup (1933).

The Atlantic water undergoes considerable mixing as it spreads across the Arctic Ocean, which results in a relatively large decrease in temperature and salinity.

The T-S curve for Station 89, representing the Beaufort Sea and the Arctic Ocean, shows that a slight warming had taken place in the upper 50 m. The remainder of the waters in the upper layers had a temperature of about -1.5°C . to a depth of 150 m. The surface layer had a salinity range of about 5 parts per mille. The Atlantic water at Station 89 had a temperature of 0.5°C . and salinity of 34.9‰ which were observed at about 500 m. Below this depth, the waters were a mixture of the Atlantic water and Arctic deep water. No Arctic deep water with characteristics as given by Sverdrup *et al.* (1942) was sampled, although these values were closely approached.

The most notable feature regarding the T-S curves for Smith Sound (23) and Viscount Melville Sound (63) is that they are nearly identical to the curve for the Beaufort Sea. The similarity between the three curves indicates that waters from the Arctic Ocean flow through these channels into Baffin Bay.

A comparison of T-S curves for the Arctic Ocean (Beaufort Sea) with those for Baffin Bay show that:

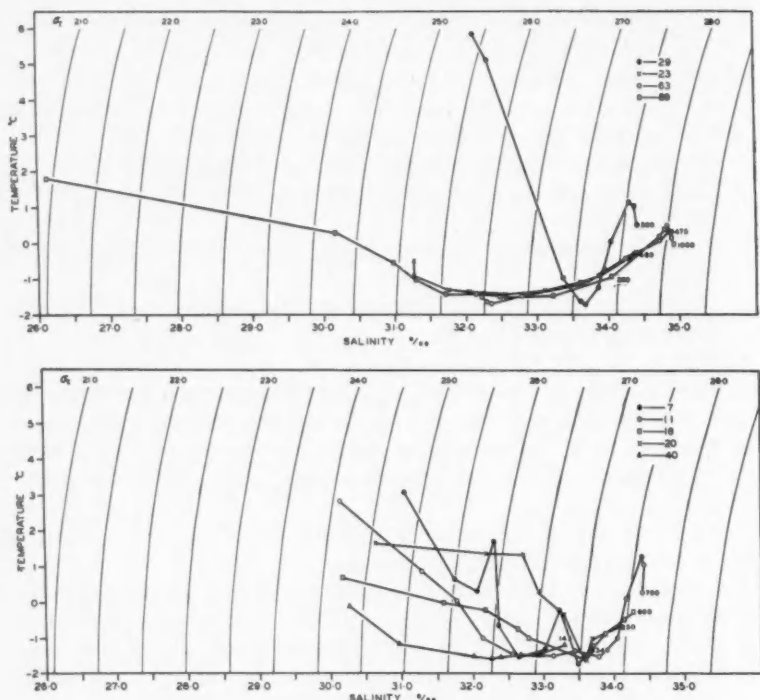


FIG. 26. (Upper) Typical T-S curves for the Canadian Arctic. (Lower) T-S curves illustrating mixing between water types in the Eastern Arctic.

1. The surface waters of the Arctic Ocean are much less saline than those found in Baffin Bay, but minimum temperatures are about the same ($-1.8^{\circ}\text{C}.$).
2. The waters in the upper 200 m. in Baffin Bay are denser than those found at corresponding depths in the Arctic Ocean.
3. Below this level, Arctic waters are the denser, and below 500 m., they are denser than any waters found in Baffin Bay.
4. Waters found at 250 m. in the Beaufort Sea and at 500 m. in Smith Sound have identical temperature and salinity characteristics ($-0.3^{\circ}\text{C}.$, 34.4‰). The waters in Central Baffin Bay as sampled by Riis-Carstensen at a depth of 1250 m. also had these temperature and salinity characteristics.

SOME EFFECTS OF SEA ICE ON OCEANOGRAPHIC CONDITIONS

The effect of drifting ice on the vertical temperature structure was shown by a comparison of bathythermograph (BT) observations taken in Prince of Wales Strait (Fig. 27).

There was only a small amount of pack ice in Prince of Wales Strait on August 30 and the vertical temperature on the eastern side of the Strait was as

shown in BT trace 166. Shortly afterward, the northern end of the strait was blocked with ice for a distance of 30 miles. The vertical temperature structure in this area on September 5 is shown by BT trace 174.

During the 5-day interval the surface waters had been cooled nearly 5 Centigrade degrees and the subsurface waters were cooled by a lesser amount. The maximum temperature of 1.7°C. in BT trace 174 occurred at about 8 m.

Assuming no exchange of water masses, the relative temperature differences between the two BT traces indicate that cooling had taken place by two separate processes. Between 8 m. and the surface the waters were chilled by direct contact with the ice and the increased vertical mixing brought about by

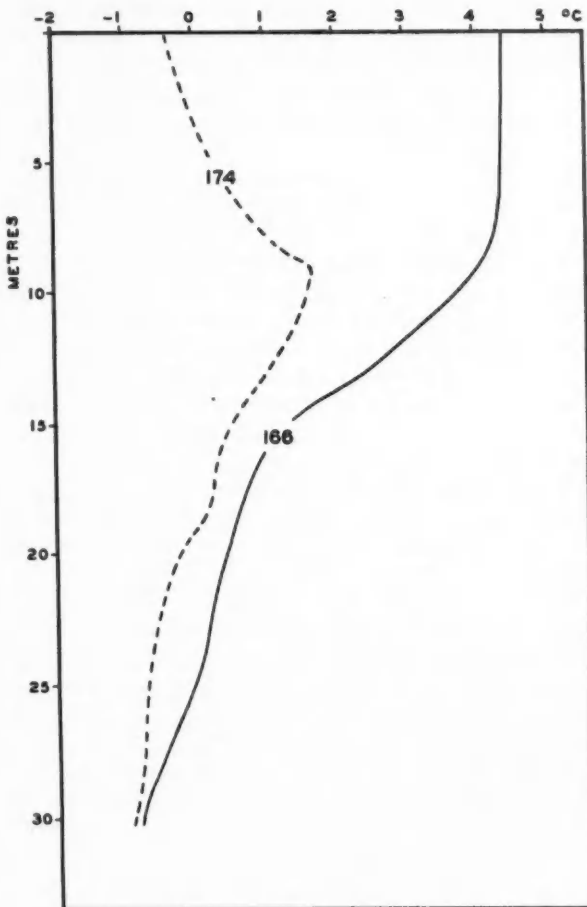


FIG. 27. Temperature-depth curves illustrating the cooling effect of drifting ice.

decreased stability. Below 8 m. the waters were cooled more slowly by the mixing that took place between the warm water and the underlying cold water.

Thus it is seen that the arrival of a mass of ice in an area which had been ice-free for some time will cause the waters to cool rapidly at the surface and slowly below the thermocline. The ultimate is an isothermal column, the depth of which will be determined by the salinity distribution in the water column.

TYPICAL TEMPERATURE-DEPTH AND SALINITY-DEPTH CURVES

Figure 28 shows temperature-depth and salinity-depth curves from selected oceanographic stations across the Canadian Arctic. The locations of the stations are shown in Fig. 2. The temperature curves are represented by solid lines and the salinity curves by dashed lines. In each case curves have been drawn to a depth of 500 m. or to the maximum observed depth in the case of the shallow

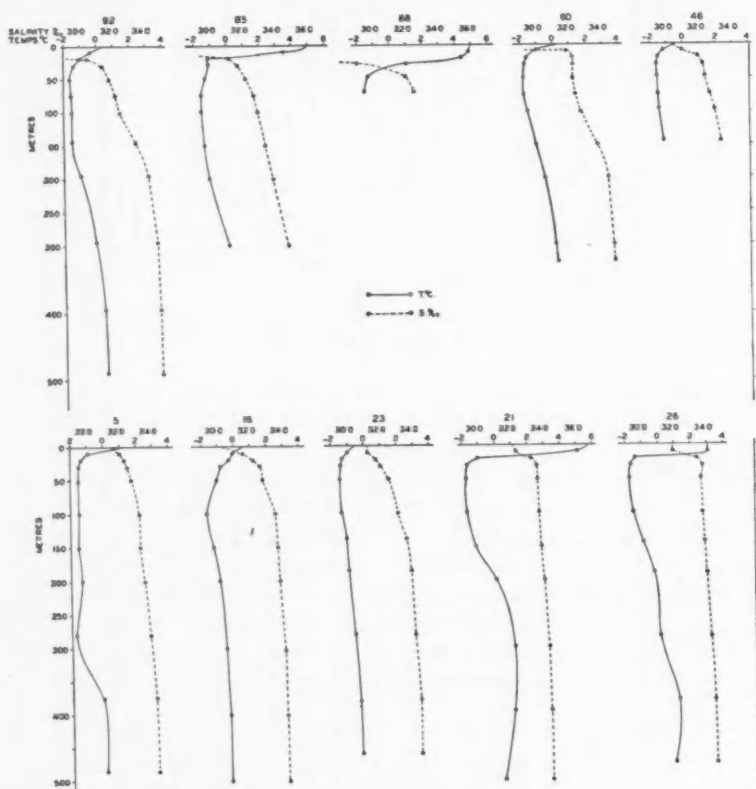


FIG. 28. Typical temperature-depth and salinity-depth curves from across the Canadian Archipelago.

stations. Surface salinities at the four westernmost stations were very low and were not plotted. The upper curves are representative of the Western Arctic while the lower ones are representative of the Eastern Arctic.

NORTH WATER

The "north water" has been defined as an area of water in the northern part of Baffin Bay and in Smith Sound, in which warm surface temperatures seem to be consistently found during the summer, and which is reported to be free of ice during all or most of the year (Dunbar, 1951). Its extent has been ill-defined as has its duration as an ice-free area. Dunbar (1951) has discussed these problems to some extent.

Mecking (1906) attributed the warm ice-free waters to an upwelling of Atlantic waters found at subsurface depths in Baffin Bay. In analysing the *Godthaab* data of 1928, Kiilerich (1933) pointed out that upwelling did not explain the presence of warm surface water, because these waters overlaid a layer of extremely cold water. The superposition of these two water types is clearly shown in Fig. 10.

Kiilerich (1933) replaced the older theory with a newer one. He postulated that the persistence of the ice-free "north water" during the winter was due to a continuous, and presumably fairly rapid, vertical exchange of water throughout the winter, the supposed heavy polar surface water from the north being, in his view, heavier than Baffin Bay water and the West Greenland remnant which penetrates as far as Smith Sound. Kiilerich emphasized that winter oceanographic research would be required to test this hypothesis (Dunbar, 1951).

Dunbar applied the researches of Hare and Montgomery (1949) on the atmospheric climate of the Eastern Arctic, to indicate the persistence of open water in the Lancaster Sound region. Monthly observations are not available to prove the existence of this open water, but the patch of warm water with a temperature above 6°C., found at the entrance to Lancaster Sound (Fig. 10 and 29), adds further evidence of its existence. The T-S curve for Station 29 (Fig. 26) indicates that the surface waters have undergone solar warming. The relatively high surface salinity (32.2‰) as compared with surface salinities in the surrounding areas (30.0 to 31.0‰) is maintained by the cyclonic circulation in that area. There is undoubtedly lateral mixing of waters as they flow around the eddy formed at the entrance. Thus there is a renewal of surface waters through a very slow process of vertical mixing. The higher temperatures and salinities would cause this area to be late in freezing over, if it did at all, and the nature of the currents would tend to keep it free of ice. Thus the area of warm water found at the entrance to Lancaster Sound may be formed locally in a manner similar to that for the open water found in other parts of Baffin Bay.

LONG-TERM CHANGES

The general warming of the Northern Hemisphere in recent years has been attributed to an increased atmospheric circulation. Hachey, Hermann and Bailey

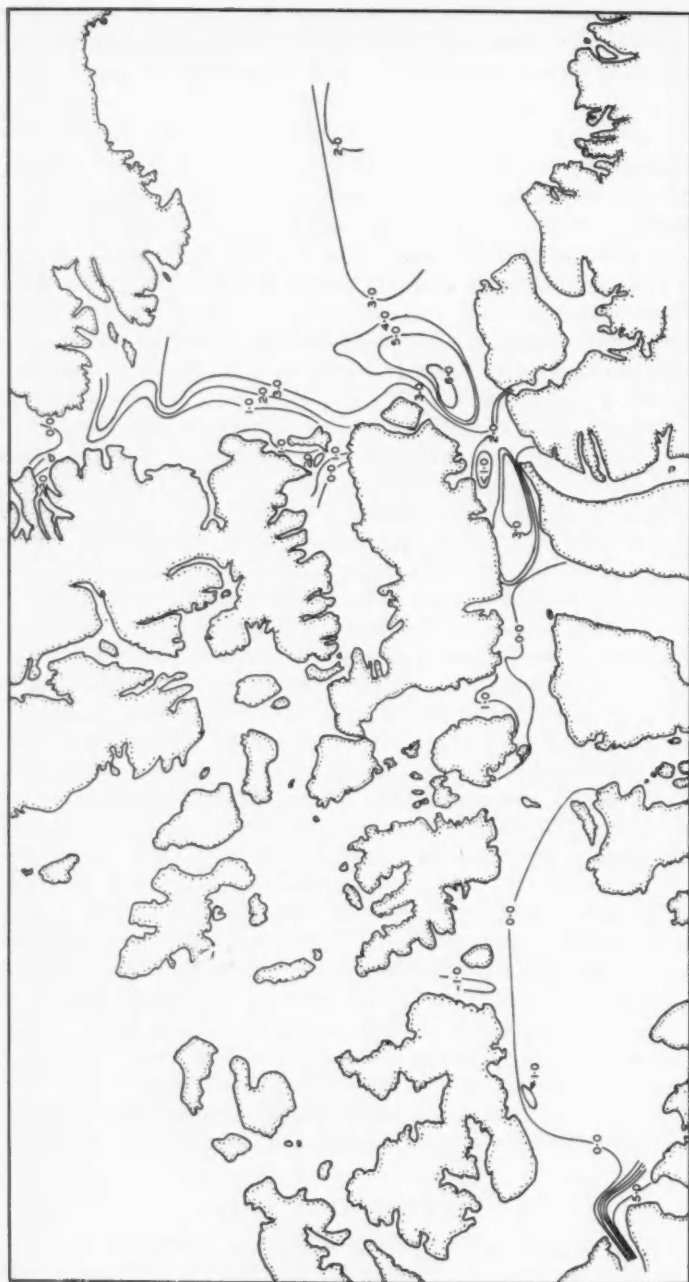


FIG. 29. Surface temperature distribution in August, 1954.

(1954) have summarized briefly the long-term changes noted in the Northwest Atlantic.

The data from *Godthaab* in 1928 and *Labrador* in 1954 are suitable for making comparisons with regard to long-term changes which may have taken place in the Baffin Bay area. Sections in Lancaster, Jones and Smith Sounds, occupied by the two ships, were closely located. The *Labrador* Sections II, V and VII are given in Fig. 3, 6 and 8, while the *Godthaab* sections are given by Riis-Carstensen (1936).

Comparisons showed that in 1954 there was less cold water ($< -1.0^{\circ}\text{C.}$) in the three sounds and a greater quantity of warm water ($> 0.0^{\circ}\text{C.}$) in Lancaster Sound than there was in 1928. Below 300 m., the waters were 0.4 Centigrade degree warmer in Jones and Smith Sounds in 1954 than in 1928 and about 0.7 degree warmer in Lancaster Sound. Corresponding salinities were about the same for the two years.

It is reasonable to assume that the influence of the Labrador Sea water entering Baffin Bay was greater in 1954 than in 1928. The waters between 300 and 700 m. were, on the average, about 0.5 Centigrade degree warmer in 1954 than in 1928. This figure is comparable to that found in Hudson Bay between 1930 and 1948 (Bailey and Hachey, 1951). An increase of 0.5 part per mille salinity was noted in Hudson Bay which was not evidenced further north.

DYNAMIC CALCULATIONS

Within the limitations imposed by shallow waters, currents have been calculated from the geostrophic equation in the manner described by LaFond (1951), and agree well with those reported by Kiilerich (1939).

The calculated velocities (Table III) in Lancaster Sound reached a maximum of 25.8 cm./sec. (0.5 knot) between Stations 4 and 5. The westward current along the north side was strong at the surface but generally weak below 30 m. The eastward current which was strongest near the centre of the sound maintained its strength to a depth of 200 m. and then decreased gradually towards the bottom.

TABLE III. Calculated average velocities at selected depths between stations located in channels leading into Baffin Bay.

Stations:	Lancaster Sound			Jones Sound		Smith Sound		
	6-5	5-4	4-3	17-16	16-15	22-23	23-24	24-25
depth (m.)	cm./sec.	cm./sec.	cm./sec.	cm./sec.	cm./sec.	cm./sec.	cm./sec.	cm./sec.
0	11.5	25.8	-15.4	3.2	14.7	-16.6	4.1	30.1
30	4.4	23.8	-2.9	-8.4	5.2	-23.1	-1.3	30.2
50	3.6	22.5	-1.1	-6.2	1.0	-23.9	-4.4	28.0
100	0.9	22.8	-0.5	0.1	-11.8	-17.1	-8.9	17.2
200	-2.0	19.5	-2.4	-0.1	-6.4	-13.9	-11.3	8.9
300	-0.3	9.8	-1.0	-0.9	-3.7	-5.7	-11.7	8.6
400	1.1	4.8	-2.1	-3.5	-2.9	0.4	-6.5	9.3
500	0.2	0.6	-0.0	-1.7	-1.3
	Reference level 600 db.			Reference level 600 db.		Reference level 500 db.		

The negative sign (—) indicates that the currents were flowing out of Baffin Bay.

In Jones Sound the current pattern indicates an eastward flow confined to the upper 100 m. on the north side with the remainder flowing westward.

The currents in Smith Sound flowed south on the Greenland side and north on the Canadian side with maximum velocities of 30.2 and 23.9 cm./sec. (0.5 and 0.6 knot), respectively. The current strengths were maintained to a depth of 400 m.

Current velocities (Table III) through Lancaster Sound show a strong eastward flow. This is continuous with the general flow pattern observed in Wellington Channel and Barrow Strait (Table IV).

TABLE IV. Calculated average velocities at selected depths in channels leading into Lancaster Sound.

Stations:	Wellington Channel			Barrow Strait	
	42-43	43-44	44-38	41-40	40-39
depth (m.)	cm./sec.	cm./sec.	cm./sec.	cm./sec.	cm./sec.
0	19.0	13.5	-0.3	2.6	-3.1
30	-2.1	12.4	-4.4	2.8	0.8
50	-6.5	7.1	-0.3	1.9	0.7
75	-7.6	5.3	0.3	1.4	0.4
100	0.7	-0.2
	Reference level 100 db.			Reference level 150 db.	

The negative sign (—) indicates that the waters were moving out of Lancaster Sound.

Kiilerich (1939) reported a net movement of water into Baffin Bay from Lancaster, Jones and Smith Sounds. His 1928 values are compared with the 1954 results in Table V.

TABLE V. Calculated volume transport through channels leading into northern Baffin Bay for 1928 and for 1954.

Section	1928	1954
	<i>m.³/sec.</i>	<i>m.³/sec.</i>
Lancaster Sound	0.64×10^6	1.48×10^6
Jones Sound	0.29×10^6	-0.39×10^6
Smith Sound	$\begin{cases} -0.03 \times 10^6 \\ 0.41 \times 10^6 \\ 0.47 \times 10^6 \end{cases}$	-0.42×10^6
TOTAL	$0.90-1.40 \times 10^6$	0.67×10^6

*Calculated by the author.

Kiilerich (1939, p. 75) chose the value of 1.4×10^6 m.³/sec. because it corresponded fairly well with the transport south into Davis Strait.

Judging from the comments made by Kiilerich regarding his dynamic calculations in northern Baffin Bay, and the large differences obtained both between data from the same year and those from different years, it is evident that in this area large variations in the volume flow take place. Just why this should be is not clearly understood. Perhaps the flow through the channels is affected by the atmospheric pressure gradient between Baffin Bay and the Arctic Ocean. The exceptional agreement between the height of the sea level and the atmospheric

pressure obtained by Sir J. Clark Ross (1854), who made simultaneous observations of the height of the sea level and the atmospheric pressure at Port Leopold in Prince Regent Inlet, would seem to bear this out.

SUMMARY

1. Inspection of the vertical distribution of temperature, salinity and density in section showed that, in the Baffin Bay area, where depths were sufficient, the water columns were composed of mixtures of four main water masses as follows:

- (a) A thin surface layer (0 to 75 m.) with temperatures generally greater than 2.0°C . and as high as 6.4°C . Corresponding salinities ranged from 31 to 32.5‰ at the surface.
- (b) A cold-water layer (20 to 350 m.) with temperatures less than -1.0°C . and as low as -1.8°C . and salinities ranging between 32.5 and 34.0‰ . The salinity corresponding to the minimum temperature was 33.7‰ .
- (c) A warm-water layer (400 to 1,000 m.) with maximum temperatures ranging from 0.5°C . to 1.3°C . and salinities of about 34.4‰ .
- (d) Deep Baffin Bay water ($> 1,000$ m.) exhibiting a temperature of -0.5°C . and salinity of 34.5‰ .

2. Inspection of the vertical distribution of temperature, salinity and density (σ_t) in section showed that in the Western Arctic and the Beaufort Sea, the water columns were composed of mixtures of four main water masses as follows:

- (a) A very thin surface layer (0 to 20 m.) with temperatures ranging between -1.0 and 2.2°C . and salinities between 4.1 and 27.4‰ .
- (b) A cold-water layer (20 to 200 m.) with temperatures less than -1.0° and as low as -1.8°C . Salinities in this layer range from 31.5‰ to 33.0‰ with a salinity of 32.3‰ at the level of the minimum temperature.
- (c) A warm-water layer (300 to 1,000 m.) with temperatures as high as 0.5°C . and salinity of 34.9‰ .
- (d) Deep water ($> 1,000$ m.) exhibiting a temperature less than -0.4°C . and salinity of 34.96‰ .

3. The origin of these waters is described as follows:

- (a) In Baffin Bay the surface layer is locally formed as is part of the cold-water layer. The upper part probably came from the Arctic Ocean. The warm-water layer had its origin in the Labrador Sea while the deep Baffin Bay water had its origin at the surface in the Arctic.
- (b) In the Western Arctic, the surface and cold-water layers are formed locally while the warm-water layers and the Arctic deep water had their origin in the Norwegian Sea.
- (c) In winter the surface and cold-water layers are identical in both areas.

4. A comparison of T-S diagrams for stations in the Beaufort Sea and in Baffin Bay shows that:

- (a) The surface waters of the Arctic are much less saline than those found in Baffin Bay, but minimum temperatures are the same ($-1.8^{\circ}\text{C}.$).
- (b) The waters of the upper 200 m. in Baffin Bay are denser than those found at corresponding depths in the Arctic Ocean.
- (c) Below 200 m., Arctic waters are the denser, and below 500 m. they are denser than any waters found in Baffin Bay.
- (d) Waters found at 250 m. in the Beaufort Sea, at 500 metres in Smith Sound, and at 1,250 m. in central Baffin Bay, have identical temperature and salinity characteristics ($-0.3^{\circ}\text{C}.$, 34.4‰).

5. Investigation of a patch of warm water at the entrance to Lancaster Sound, exhibiting a temperature greater than $6.0^{\circ}\text{C}.$ with a salinity of 32.2‰ , revealed that it was the same water which is identified as "north water".

6. Dynamic calculations of current velocities in Lancaster, Jones and Smith Sounds give a good agreement with those of Kiilerich (1939) for the 1928 *Godthaab* data. Dynamic calculations show wide variations in the net transports through various channels which may be attributed to meteorological causes.

ACKNOWLEDGMENTS

The author wishes to acknowledge the encouragement and counsel freely given by Dr. H. B. Hachey and Dr. H. J. McLellan, and the excellent co-operation and comradeship tendered by Captain O. C. S. Robertson, R.C.N., Dr. D. C. Rose, Cmdr. J. M. Leeming, R.C.N., and all of the officers and men of H.M.C.S. *Labrador*. The cheerful and faithful assistance given by Mr. J. G. Clark and Mr. C. C. Cunningham in collecting the data is most appreciated.

The observations discussed herein were made possible through the co-operation of the Defence Research Board of Canada, the Royal Canadian Navy, and the Canadian Joint Committee on Oceanography. This paper is published with the sanction of the Canadian Joint Committee on Oceanography.

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The Effect of Certain Antibiotics on the Production of Trimethylamine and Hydrogen Sulphide by Bacterial Enzymes¹

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ABSTRACT

By the use of the washed cell technique it has been shown that the antibiotics chlortetracycline, oxytetracycline, polycycline and nisin in concentrations from 1 to 50 p.p.m. do not retard the bacterial reduction of trimethylamine oxide to trimethylamine. It has also been shown that chlortetracycline and oxytetracycline do not inhibit the reduction of cysteine to hydrogen sulphide by bacterial enzymes.

INTRODUCTION

Food preservatives have several modes of action in preventing or retarding spoilage caused by bacteria or other micro-organisms. They may be either bactericidal or bacteriostatic; or they may act on one or more of the non-vital enzyme systems of the micro-organisms, thus interfering with some of their chemical activities, without necessarily preventing the growth and multiplication of the organisms. If the products of their uninhibited enzyme systems happen to have particularly unpleasant flavours or odours, inhibition through action of a preservative will help delay at least this aspect of spoilage of the food product.

It is known that the antibiotics now being recommended for the preservation of fish and other foods do have a marked bacteriostatic action on the spoilage bacteria. This paper deals with their action on two of the enzyme systems that are concerned with the spoilage of certain sea fish. The antibiotics used were chlortetracycline (American Cyanamid Co.), oxytetracycline (Chas. Pfizer and Co.), polycycline (Bristol Laboratories) and nisin (Aplin and Barrett Ltd. of England). The enzyme systems studied were those concerned with the reduction of trimethylamine oxide to trimethylamine and the reduction of organic sulphur compounds to hydrogen sulphide.

EXPERIMENTAL

The method used to test the inhibition of the enzymes consisted in adding the antibiotic to a preparation of washed bacterial cells in a buffer solution containing the appropriate substrate and comparing the rate of enzyme activity with similar systems minus the antibiotic. The trimethylamine was measured colorimetrically by the method of Dyer (1945, 1950) and the hydrogen sulphide by the method of Fischer (1883) as modified by Brenner *et al.* (1953).

¹Received for publication January 16, 1957.

REDUCTION OF TRIMETHYLAMINE OXIDE

Two cultures were used in this test. The first was one of *Serratia marcescens*, which reduced trimethylamine oxide fairly rapidly. The second was from an unidentified gram negative rod (No. 216) isolated from the fish, and which reduced the oxide more rapidly. The reaction mixture contained:

- 2 ml. of 0.2 M trimethylamine oxide ($(\text{CH}_3)_3\text{NO}$,
- 2 ml. of 0.2 M sodium acetate,
- 3 ml. of 0.2 M phosphate-sodium hydroxide buffer, pH 7.2,
- 4 ml. of washed bacterial cells.

In the first group of experiments, each of the four previously named antibiotics was tested individually at concentrations of 5, 25 and 50 p.p.m. in the reaction mixture made up to contain 45.5 mg. dry weight of *S. marcescens* cell suspension per millilitre. The control tubes contained no antibiotic. None of the four antibiotics at any of their three concentrations caused any retardation in the rate of reduction of trimethylamine oxide to trimethylamine, as judged by comparison of their rate curves with that of the control reaction mixture.

The second group of experiments was with chlortetracycline only, at concentrations of 1, 5, 10, 25 and 50 p.p.m. in the reaction mixture containing 33.1 mg. dry weight of culture No. 216 cell suspension per millilitre. In this case also the antibiotic had no effect, at any of its five concentrations, on the rate of trimethylamine production.

The pH of the reaction mixture was adjusted in all of these tests to 7.2 which is near the optimum for reduction of the oxide by bacterial enzymes (Castell and Snow, 1949; Elliott, 1952). Another set of tests was made with chlortetracycline (50 p.p.m.) in substrates similar to those described above, except that the buffers were changed to give eight pH values ranging between 6.0 and 8.0, using cells of culture No. 216.

The results showed that within the pH range used, the antibiotic did not inhibit the reduction of the oxide, although the different pH values had a marked effect on the rate of the oxide reduction by the bacterial enzymes as has been found previously (Castell and Snow, 1949).

REDUCTION OF CYSTEINE

The culture used for testing the effect of the chlortetracycline and oxytetracycline on the enzymic reduction of cysteine was *Escherichia coli*. The hydrogen sulphide was removed from the cell suspensions by a current of carbon dioxide after acidification with hydrochloric acid. It was then absorbed in a zinc acetate solution and combined with *p*-amino dimethylaniline, hydrochloric acid and ferric chloride to form methylene blue, which was measured with an Evelyn colorimeter using a 660-m μ filter.

Once again the results were entirely negative. Neither the chlortetracycline nor the oxytetracycline in concentration of 50 p.p.m. retarded the reduction of cysteine by washed cells of *E. coli*.

DISCUSSION

Sodium nitrite is the preservative now most extensively used for fresh fish in Eastern Canada. Under acid conditions sodium nitrite can be either bactericidal or bacteriostatic. Under slightly acid, neutral or alkaline conditions sodium nitrite has little or no effect on the growth of fish-spoiling bacteria, but it does inhibit the enzymic reduction of organic sulphur compounds to form hydrogen sulphide (Richards, 1951) and the reduction of trimethylamine oxide to form trimethylamine (Castell, 1949). Certain other enzymes active in the decomposition of fish are not inhibited by the nitrite. The result is that although nitrite may have some inhibiting action on the development of spoilage by retarding bacterial growth, its chief value seems to be that it changes the pattern of spoilage by eliminating the production of certain unpleasant volatile compounds.

The action of nitrite on the reduction of trimethylamine oxide is of particular interest to those concerned with measuring the quality of fish flesh. It has been found that trimethylamine is one of the most useful measures of the earlier stages of spoilage in Atlantic coast cod, haddock and many other marine fish.

The trimethylamine content has been suggested as one of the main criteria to be used in determining the quality of cod and haddock under the grading program currently being considered by the Department of Fisheries of Canada. However, trimethylamine loses all meaning as a measure of spoilage when applied to fillets that spoil subsequent to their treatment with sodium nitrite (accompanying Table). This means that if we continue to use nitrite we must have one set of criteria for spoilage for round fish, dressed fish, and untreated fillets, and another for nitrite-treated fillets. It is estimated that over 90% of the fresh fillets now being shipped to central Canada from the Atlantic coast are treated with nitrite.

Therefore, from an analytical standpoint, the use of these antibiotics has an added advantage over sodium nitrite as a fish preservative, in that they do not

Trimethylamine values² of nitrite-treated and untreated fillets taken from retail stores in Ontario. In each group an effort was made to select 10 fresh fillets free from all signs of spoilage and 10 fillets that were spoiled or spoiling.

Nitrite-treated		Untreated	
Fresh	Spoiled	Fresh	Spoiled
1.8	2.0	0.8	34.0
1.2	6.0	2.8	18.4
3.0	1.2	1.3	33.2
0.8	1.5	3.4	35.0
0.8	1.6	0.2	11.0
0.6	0.9	0.8	8.5
2.1	0.1	0.7	27.0
1.4	0.9	2.1	49.0
0.1	2.6	2.8	48.0
2.8	1.1	2.1	13.0

²Trimethylamine values are expressed as milligrams of trimethylamine nitrogen per 100 g. of fish.

inhibit the enzymic reduction of trimethylamine oxide. This means that if the nitrite is replaced with one of the tetracycline antibiotics, it will then be possible to use trimethylamine as an objective measure of quality, not only for fish at the coast, but also in the wholesale and retail stores in the larger consumer areas in central Canada. This in turn may eliminate one of the major problems in the currently proposed set-up and in the grading and quality control of many species of marine fish.

There is always the possibility that an antibiotic may change the spoilage pattern in fish by a selective bacteriostatic action. So far as we know, however, there are no data showing this to be the case with the broad-spectrum antibiotics such as chlortetracycline or oxytetracycline.

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The Action of *Pseudomonas* on Fish Muscle: 2. Musty and Potato-like Odours¹

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ABSTRACT

Bacteria producing musty and potato-like odours have been isolated from fillets of cod and haddock and identified as *Pseudomonas perolens* Turner. They are psychrophilic and are able to produce their characteristic odour on a wide range of substrates.

INTRODUCTION

THE introductory paper of this series (Castell and Greenough, 1957) described a number of different odours that commonly develop during the earlier stages of spoilage in chilled fish muscle, and showed that the causal organisms belonged to the genus *Pseudomonas*. This present paper deals with one specific group of these spoilage odours and identifies and describes the bacteria that produce them. The odours under consideration here are those commonly characterized as being "musty". When they are more concentrated, and especially when produced from pure cultures, they have a striking similarity to the odour of stored potatoes.

This "potato" odour has been observed under commercial conditions on chilled fillets of cod, haddock, and flounder as well as on halibut steaks. Only very rarely is it the predominating odour on normally contaminated fish. Usually it is accompanied by sour, fruity or onion-like odours, to which it adds a characteristic mustiness. It has never been observed on fresh or spoiling round or gutted fish, although the causal organisms have been isolated from the surface slime of iced cod and haddock. The odour is most frequently encountered from colonies growing on nutrient agar plates that have been prepared for making bacterial counts from iced fillets.

CULTURAL CHARACTERISTICS

Table I summarizes the cultural characteristics of these "potato" organisms. In general they are very inert. They are neither proteolytic nor lipolytic; they do not ferment sugars and they do not reduce trimethylamine oxide. They produce little or no observable change in milk and they reduce neither nitrate nor nitrite. They produce ammonia from peptone, various amino acids and from urea. They produce hydrogen sulphide from cystine and methionine, but none or only traces from thiosulphate. They are very definitely psychrophilic, growing at all temperatures between 0 and 25° C. but not at 37° C. or above.

¹Received for publication January 16, 1957.

TABLE I. Cultural characteristics of a green fluorescent *Pseudomonas* isolated from chilled Atlantic cod fillets and producing a potato odour.

Gram-negative, motile rods with polar flagella and no spores.
Agar colonies: circular, smooth, cream-coloured and green, water-soluble pigment.
Proteins (casein, gluten, gliadin, zein): not hydrolyzed.
Gelatine: not liquified.
Fats (fish oil, butterfat, triolein, tributyrin): not hydrolyzed.
Lecithin not hydrolyzed.
Litmus milk: slowly reduced but no other change.
Indole not formed.
Acetylmethylcarbinol not formed.
Nitrate and nitrite not reduced.
Nitrite not formed from hydroxylamine.
Ammonia from peptone and asparagine.
Trimethylamine not formed from either trimethylamine oxide or choline.
Cellulose, starch, inulin, and dextrin not hydrolyzed.
Acid, but no gas, from dextrose, D-mannose, and D-galactose.
Neither acid nor gas: lactose, sucrose, maltose, L-arabinose, cellobiose, rhamnose, levulose, L-xylose, D-mannitol, raffinose, dulcitol, glycerol, inositol, sorbitol, salicin, or ethanol.
H ₂ S produced from tryptone, L-cystine, and DL-methionine, but none or only a trace from sodium thiosulphate.
Decomposes urea to form ammonia.
Temperature range: grows slowly at 0° C., fair at 5 to 10° C., rapidly at 10 to 25° C., no growth at 37° C. and above.
Odour: produces a strong musty, potato-like odour on milk, broth, nutrient agar and many other substrates.

The comparison of cultural characteristics shown in Table II would suggest that the "potato" organism isolated from fish is similar to the bacteria isolated by Spanswick (1930), producing a musty odour in eggs, and a similar organism isolated by Jensen (1948) producing musty odours in some chilled meats. Both these workers classified their isolates as *Achromobacter perolens*. Szybalski (1950) later pointed out that as the so-called *Ach. perolens* produces a green, water-soluble pigment and has a single polar flagellum, it should be classified as *Pseudomonas perolens*.

Other organisms producing potato-like odours have been isolated before. Levine and Anderson (1932) quote Jenkins and Hendrickson (1918) as having isolated from musty eggs organisms that produced an earthy odour resembling "old fillers and flats", while at other times it seemed more like that from *sprouting potatoes*, or spoiled hay or chaff. Olson and Hammer (1934) isolated from milk organisms which produced a decidedly potato-like odour.

A survey of the literature shows that many of the musty-odour-producing organisms lose their ability to produce this characteristic odour after repeated transfer on nutrient agar. This was the case with the organisms isolated by Turner (1927) and Jensen (1948), but not with those isolated by Spanswick (1930). The organisms we have isolated from fish have been transferred on nutrient agar approximately every 2 months for 6 years and are stored at 0 to 2° C. They still retain their ability to produce the odour without any apparent diminution of intensity. It has been noticed, however, that the composition of the substrate as well as the pH have a marked influence on the production and intensity of the odour.

TABLE II. Differential characteristics^a of bacteria producing musty and/or potato-like odours (adapted from Jensen, 1948).

Author	Source	Identified as	Motile	Growth at 37° C. 10° C.	Gelatin lig.	Acid in milk	NO ₂ to NO ₃	Acid in			Fluores- cence
								Lactose to NO ₂ (5 days)	Arabi- nose (5 days)	Rhamnose (20 days)	
Turner (1927)	Eggs	<i>Ach. perolens</i>	+	-	+	-	+	-	+	-	?
Spanwick (1930)	"	ditto	+	+	-	+	-	+	-	+	+
Levine and Anderson (1932)	"	<i>Ps. graveolens</i>	+	+	-	+	-	+	-	-	-
ditto	"	<i>Ps. mucidolens</i>	+	+	+	-	+	-	+	Alk.	-
ditto	"	<i>Ps. mucidolens</i> var. <i>tarda</i>	+	+	+	+	+	+	+	+	-
Jensen (1948)	Poultry skins	<i>Ach. perolens</i>	+	+	-	+	+	-	-	-	+
ditto	Veal rolls	ditto	+	+	-	+	-	-	-	-	+
ditto	Beef and veal	<i>Ps. graveolens</i>	+	+	-	-	-	+	+	+	+
ditto	Pork loins	ditto	+	+	-	+	-	+	+	+	+
Olson and Hammer (1934)	Poultry meats	<i>Ach. perolens</i>	+	+	-	+	+	-	+	+	-
ditto	Milk	<i>Ps. graveolens</i>	+	+	-	+	+	-	+	+	-
Present paper (1956)	"	<i>Ps. mucidolens</i>	+	+	-	+	-	-	-	-	+
ditto	Fish	<i>Ps. perolens</i>	+	+	-	+	-	-	-	-	+

^a - Indicates negative reaction; + indicates positive reaction.

EXPERIMENTAL

FACTORS INFLUENCING THE PRODUCTION OF THE POTATO ODOUR
HYDROGEN ION CONCENTRATION

The pH of the substrate can affect the production of a specific odour-producing compound in two ways. It can affect the initial elaboration of the compound by inhibiting the bacterial enzymes; in some cases it can also determine whether the compound will be held as a salt or released as a free acid or base. Experiments have been carried out to determine the effect of pH on the production of the potato-like odour as well as the effect of pH on the odouriferous compound when already present.

Both broth and agar media were prepared, containing the usual mineral salts and 1% each of sodium acetate and Bacto asparagin. These were buffered by adding KH_2PO_4 -NaOH solutions to give pH values ranging from 6.1 to 8.0 and were sterilized in screw-capped bottles. After inoculation with the "potato" organism they were incubated at 8 to 10° C. Periodically the cultures were examined for the extent of growth and odour production. Determinations for pH were made periodically on the broth cultures but not on the agar slants. The results are summarized in Tables III and IV. It can be seen that after 6 days in the broth at 8 to 10° C. there was no growth at pH 6.4 and below, and only slight growth at pH 6.8. At pH 7.3 to 8.0 the organisms grew well. The optimum pH range for the growth of this organism is definitely above the neutral point. If the odour production is examined without taking into consideration the extent of growth, it would appear that it too is definitely favoured by an alkaline reaction. However, from these data it is difficult to dissociate these two factors. All that we can be sure of is that those pH values which produced the best growth also favoured the production of the odour and that at first the odours were musty and when more concentrated became potato-like. Table IV shows the effect of raising the incubation temperature from 8 to 10° C. up to 25° C. In addition to the potato odour, all the cultures in the alkaline range smelled of ammonia.

In buffered broth samples (Table III) there was not much change in the pH of broth after 6 days at 8 to 10° C. In similar, unbuffered media the pH rose

TABLE III. Effect of pH on growth of, and odour production by *Ps. perolens* (isolated from fish), growing on an asparagine broth.

Initial pH	After 6 days at 8 to 10° C.		
	Growth ^a	pH	Odour
6.15	-	6.13	Slight
6.40	-	6.35	Slight
6.80	+?	6.90	Slight
6.98	++	7.05	Slight
7.20	++	7.45	Musty plus potato-like
7.38	+++	7.60	Potato-like
7.75	+++	8.00	Strong potato-like
8.00	+++	8.00	Strong potato-like

^aIndicates none observable; +? scanty; ++ good; +++ abundant.

TABLE IV. Effect on pH on growth of, and odour production by *Ps. perolens* (isolated from fish), growing on an asparagine agar.

Initial pH	After 1 day at 8 to 10° C.		After 1 day at 8 to 10° C. plus 1 day at 25° C.		After 1 day at 8 to 10° C. plus 2 days at 25° C.	
	Growth ⁴	Odour	Growth ⁴	Odour	Growth ⁴	Odour
6.10	—	Sour	—	Sl. sour	?	Sour
6.45	—	Sl. sour	—	Sl. sour	++?	Slight
6.80	++?	Slight	+	Slight	++	Potato
7.00	++	Musty	++	Musty	+++	Strong potato plus NH ₃
7.20	++	Musty	++	Strong potato	+++	Ditto
7.45	++	Musty	++	Ditto	+++	Ditto
7.85	++	Musty plus potato	++	Ditto	+++	Ditto
8.00	++	Potato	++	Strong potato and sl. NH ₃	+++	Strong potato plus strong NH ₃

⁴Significance of symbols same as in Table III.

slowly at first, but after considerable incubation, and accompanying a very intense potato odour, the pH rose to values of 8.0 and above.

In the second set of tests the organisms were grown on nutrient agar until they had developed a very intense potato odour. Washings from the surface of these cultures provided a suspension of cells and soluble material extracted from the agar that had a very intense potato odour. One millilitre of this suspension was added to each of a series of 20 ml. of buffer solutions ranging between pH 5.0 and 12.0 and examined for odour. The judges had no idea of the pH values of the samples they were examining. The results were as follows: (The pH values given are those of the buffer-suspension mixture at the time of examination for odour.)

pH	Odour
5.1	Potato plus sweetish
5.9	ditto
6.1	ditto
6.3	ditto
6.7	Potato plus more intense sweetish suggestive of chloroform
7.1	Potato
7.6	Potato
9.8	Stronger potato
12.2	Very strong potato

Test paper soaked in a pH indicator, suspended above the liquid, showed that volatile base was being formed by the "potato" cultures. The addition of formaldehyde immediately stops the release of this volatile base—indicating that it is probably ammonia. Ammonia-like odours have frequently been identified along with the potato odour in later stages of growing cultures and probably help to account for the difference in odour for acid and alkaline reactions. However, the characteristic potato odour is present at all pH values between 5 and 12.

SUBSTRATE

In order to determine the effect of the composition of the substrate on the production of odour, a basic medium was prepared by using 0.1% each of MgSO_4 and K_2HPO_4 , 0.5% NaCl and 1% agar. To this was added 1% of the ingredients to be tested and the pH then adjusted to approximately 7.4 with a solution of NaOH . After autoclaving in screw-capped bottles these were slanted, inoculated, and incubated at 8 to 10° C. Some sets were also incubated at 0 and 25° C.

A characteristic potato odour was obtained following growth on each of these complex protein-containing substances: Bacto beef extract, yeast extract, peptone, tryptone, liver, veal, beef blood, egg albumin, milk powder and gelatin. No growth was obtained with purified gluten, gliadin, zein, or casein.

Abundant growth and strong potato-like odour occurred on vitamin-free hydrolysates of soy protein, yeast, casein and lactalbumin. With some of these materials, other odours as well as the potato odour developed; for example, on tryptone and the hydrolysates of casein and lactalbumin there was a distinct turnip-like odour at one stage; the casein hydrolysate also developed a slight garlic-like odour and later a strong odour of ammonia.

In every instance where the organisms grew on these complex substrates the characteristic potato odour developed, but it was much stronger on some than on others. It was especially strong from beef extract, yeast extract, peptone, tryptone, and the hydrolysates of lactalbumin and yeast. There was the least odour from gelatin.

The abundant growth and strong odour from the protein hydrolysates suggested that certain of the amino acids may be responsible. The separate addition of a number of individual amino acids to the above-mentioned basic medium, but to which 0.2% sodium acetate was also added, resulted in growth and odour production from these amino acids as indicated in Table V. It shows that the production of the potato-like odour occurred with almost every amino acid that supported growth of the inoculant. In addition, however, there were many other odours. With many of the amino acids that supported vigorous growth the original "stored potato odour" changed into a very intense odour suggesting the cut flesh of green or unripe potatoes. This was also described by some of the observers as the "odour of potato sprouts". This "green potato" odour persisted with the cultures for many weeks. It was never observed in the absence of strong green or yellow-green fluorescent coloration of the medium. Some of the other odours that were noted from the action of the organism on specific amino acids were: DL-phenylalanine—hyacinths; DL-valine and DL-leucine—rotten hay; DL-methionine—rotten cabbage; DL-asparagine—sweet; hydroxy-L-proline and DL-valine—roasted peanuts. Some of the uninoculated, autoclaved media containing amino acids had slight characteristic odours, notably: DL-methionine, DL-phenylalanine, DL-leucine, and DL-isoleucine; but they were much less intense and often quite different from the odours of the inoculated samples.

When sodium or ammonium nitrate was used in the same basic medium in place of the amino acids, growth was at first retarded, but ultimately it became

TABLE V. Growth of, and odour production by *Ps. perolens* (isolated from fish), growing on a basic medium plus 1% of various amino acids^a and adjusted to pH 7.3.

Amino acid	Growth ^b	Water-sol. pigment	Potato odour	Other odours
Beta-alanine	+++	+++	+++	>Green potato >NH ₃
DL-valine	+++	+++	+++	>Green potato >spoiling hay
Hydroxy-L-proline	+++	+++	+++	>Green potato >sweaty woollen socks
DL-asparagine	+++	+++	+++	>Green potato >ammonia
DL-serine	+++	+++	+++	>Green potato
DL-alpha alanine	+++	+++	+++	>Green potato
Betaine	+++	+++	+++	>Green potato
DL-phenylalanine	++	+++	+++	Hyacinth > green potato
DL-leucine	+++	+++	+++	Green potato + spoiling hay
DL-methionine	+++	-	++	Spoiled cabbage
DL-norleucine	++	-	++	Amyl acetate, musty
Amino acetic acid	++	-	+	Sweaty woollen socks
Tyrosine	+++	-	+	-
Creatine	++	+	+	Musty
DL-threonine	+	-	++	Sl. green potato, musty
DL-tryptophane	+	-	++	-
L-cystine	+	-	Not much odour	Sl. rotten potato
L-tyrosine	+	-	ditto	-
Alpha amino n butyric acid	-	-	ditto	-
Cysteine	-	-	-	Sl. H ₂ S
L-Arginine	-	-	-	-

^a Obtained from Eastman Kodak Co., Rochester, N.Y.^b - Indicates no growth, pigment, or odour;

+ Indicates growth, pigment, or odour, slight;

++ Indicates growth, pigment, or odour, fair;

+++ Indicates growth, pigment, or odour, abundant.

abundant and there was a strong potato odour. Nitrate with glycerol and the mineral salts also produced good growth and the characteristic odour. No growth occurred using ammonium acetate as the sole source of both carbon and nitrogen.

There was slight and retarded growth with urea as the nitrogen source, without the production of odour. There was also slight growth and a slight odour of potato with xanthine as the nitrogen source.

In the pH range of 6.5 to 8.0 the addition of 200 p.p.m. sodium nitrite did not inhibit either the growth of the organism or the production of the characteristic odour.

SUMMARY AND DISCUSSION

Cultures of bacteria have been isolated from fresh and spoiling fish muscle that develop a characteristic musty odour which later develops into an odour that is very characteristic of stored potatoes. These organisms have been identified as *Pseudomonas perolens* Turner. The same species appears to have been isolated and identified by Spanswick (1930) from musty eggs and by Jensen (1948) from musty meats. Similar or closely related organisms have been isolated by other workers from foods having musty or potato-like odours.

The characteristic potato odour has been produced by growing *Ps. perolens* on a wide range of culture media. Protein hydrolysates and many of the amino acids are particularly good substrates both for growth and odour production.

However, the organisms are able to produce the odour with sodium nitrate as the sole source of nitrogen and sodium acetate or glycerol as the sole source of carbon.

One outstanding characteristic of this organism is its ability to grow at low temperatures; another is its general inertness on purified proteins, fats, sugars, and many carbohydrates. It does not reduce trimethylamine oxide.

The production of the potato odour by *Ps. perolens* is not inhibited by the addition of sodium nitrite.

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Some Effects of Kraft Mill Effluent on Young Pacific Salmon¹

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ABSTRACT

Sockeye salmon underyearlings (*Oncorhynchus nerka*) were exposed to various concentrations of full-bleach kraft mill effluent under experimental conditions simulating those anticipated in the estuary of the Somass River at the head of Alberni Inlet, B.C. An anticipated expanded production of a kraft pulp mill discharging effluent into this area was regarded as a potential source of pollution which could influence survival of young salmon migrating into and through the estuary. A 4.8% concentration of effluent by volume in sea-water of 20‰ salinity at 17.8° C. was a limiting concentration for toxicity, below which survival was complete and independent of length of exposure. However, when oxygen requirements for respiration were considered and were compared with net oxygen availability after effluent oxidation in the area, the interaction of toxicity of the effluent and lowered oxygen availability suggests that the limiting concentration of effluent in this particular case be lowered from 4.8 to 2.5% effluent.

INTRODUCTION

THE toxicity of a sulphate effluent to young sockeye salmon (*Oncorhynchus nerka*) was determined as part of a study to provide information on "safe" concentrations of effluent, discharged from a kraft mill situated at the head of Alberni Inlet, B.C. Three species of Pacific salmon including the sockeye (*O. kisutch.*), and spring (*O. tshawytscha*) migrate through the area into the Somass River as spawning adults, from June to late October. Their progeny return to the sea mostly during the spring and summer months. Minimum levels of river discharge occur in August and September, resulting in maximum effluent concentrations. At this time temperatures and salinities are highest, factors which must be considered in their influence on toxicity relations.

Summer temperatures and salinities at the head of Alberni Inlet were taken as type conditions for experimental simulation. Detailed studies of the pollution potential in that area have been carried out by Tully (1949) and Waldichuk (1954a) with particular reference to the effluent discharge of the mill, its dilution, oxidation requirements and path of seaward movement.

Estimates of toxicity and oxygen requirements are provided from experimental evidence, for various levels of effluent concentration. Physical evidence reported by Waldichuk (*loc. cit.*) is used in conjunction with these data to provide an estimate of limiting effluent levels for safe passage of seaward salmon migrants through the Somass River estuary.

MATERIALS AND METHODS

Assays were conducted in sixteen 11-litre glass bottles consisting of pairs of seven concentrations of a 24-hour composite sample of effluent, and two controls.

¹Received for publication February 5, 1957.

Wax-lined tops to the containers were drilled to provide a small hole through which motor-driven stirrers afforded circulation of the solutions yet inhibited free contact of their contents with the air. Test solutions were made up to 2, 5, 6, 7, 8.5, 10 and 18% effluent by volume. These solutions were renewed every twelve hours, using 24- to 36-hour-old refrigerated effluent and sea-water adjusted to a salinity of 20‰. Immediately before and after each exchange, oxygen concentrations were determined. Five fish were started in each solution and these were fed once daily prior to the renewal of the test solutions.

Sockeye underyearlings cultured at the Biological Station and used in the assays averaged 5.04 cm. fork length, 1.19 g. in weight and averaged 0.48 g. of fish per litre of solution. Experimental conditions associated with the tests are listed in Table I.

TABLE I. Acclimation and test temperatures and salinities for sockeye salmon underyearlings in assays for resistance to kraft mill effluent.

Temperature acclimation	raised to 18° C. for 15 days from an average temperature of 14° C.
Salinity history	taken from fresh water and put at 20‰ for 15 days
Test temperature, average	17.8° C.
Test temperature, range	17.3-18.2° C.
Test salinity, average	19.48‰
Test salinity, range	14.08-22.25‰

Full-bleach kraft effluent was obtained from the Harmac mill near Nanaimo, B.C. This mill, like the kraft mill at Alberni, is operated by MacMillan and Bloedel Ltd., but discharges its effluent into a tideswept channel. The composition of the Harmac mill effluent is comparable with that from the proposed production of the Alberni mill. Data on effluent composition is reproduced in Table II.

TABLE II. Data from August 2-19, 1954, on the composition of the effluent used in the assays (by permission of MacMillan and Bloedel, Ltd., Harmac Mill). Values for black liquor are based on analysis of black liquor samples taken August 5, 1954, by Dr. M. Waldichuk, Fisheries Research Board.

Characteristic	Average	Range
pH	5.07	3.75-6.70
Average Cl ₂	negligible	
Sulphidity, ppm.	15.2	13.5-16.5
Dissolved solids, ppm.	872	446-1022
Volatile solids, ppm.	322	252-514
Black liquor, ppm.	1536	1170-2460

Some difficulty was experienced in maintaining dissolved oxygen in the closed containers, even with renewal of the solutions at twelve-hour intervals. Dissolved oxygen values before and after renewal of the solutions averaged 3.90 and 7.62 ppm., respectively (41 and 78% saturation at the average test temperature.)

Cessation of respiratory movements and immobility were taken as the criteria of death.

RESULTS

TOXICITY OF THE EFFLUENT

Probit-response log mortality-time curves for the concentrations from 5 to 18% effluent are illustrated in Fig. 1 as a visual indication of goodness of fit.

The slope of the 10% line appears to be anomalous. In such series, the slope is usually directly related to the magnitude of the stimulus. To relate the slope of this line to the family of slopes in the series, the line has been rotated about its geometric mean. Although the departure of the slope of the 10% line from the series leaves the line suspect, it is retained for the information it may contribute, on the assumption that a measure of central tendency obtained from

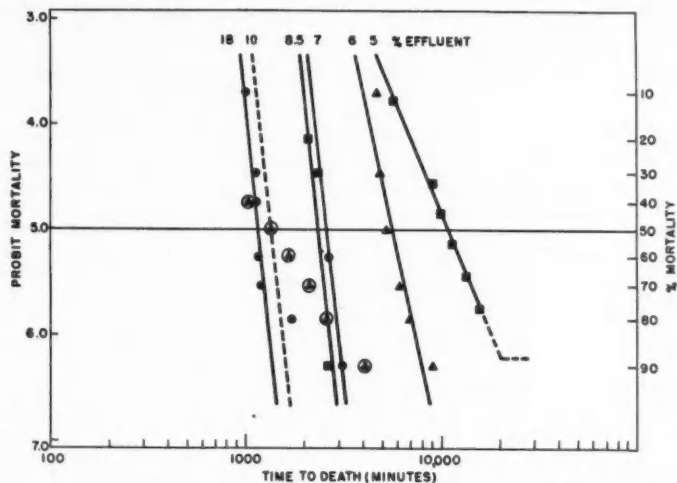


FIGURE 1. Time-mortality curves for sockeye salmon underyearlings exposed to various concentrations of kraft mill effluent. The figures in the graph represent percentage effluent in the several dilutions. For explanation of the figure, see the text.

the line will be least affected by the anomaly. Equally evident are problems in grouping of the data in the 7 and 8.5% effluent concentrations leading to lessened sensitivity in estimation of the median survival times. There is also a possibility that the 5% effluent line is truncated, although the condition of the survivors at the end of the experiment suggests that they would have died eventually. The position of all lines other than that for the 10% effluent group has been estimated by derivation of the provisional curves after the method of Bliss (1952).

Preliminary analysis of the data was carried out to linearize the relation between survival time and effluent concentration, and to stabilize the variances. Means and standard deviations of the distribution of survival times at each effluent concentration were calculated from the original data expressed as

logarithms and reciprocals. Calculation of correlation coefficients for a measure of association between mean and standard deviation in the reciprocal and logarithmic series yielded values of $P \approx 0.90, 0.85$ respectively. Accepting the null hypothesis in both cases, the reciprocal transformation has been retained for its slightly improved measure of independence. A tendency remains toward inconstancy of the variances arising mainly from the 10 and 18% effluent concentrations. The anomaly in the former has been indicated. In the absence of further data, no attempts were made to refine the analysis in this regard and the remaining variance heterogeneity was accepted as qualifying the results.

When the harmonic mean survival time is plotted against effluent concentration, the resulting distribution resembles a rectangular hyperbola (Fig. 2), with the general formula:

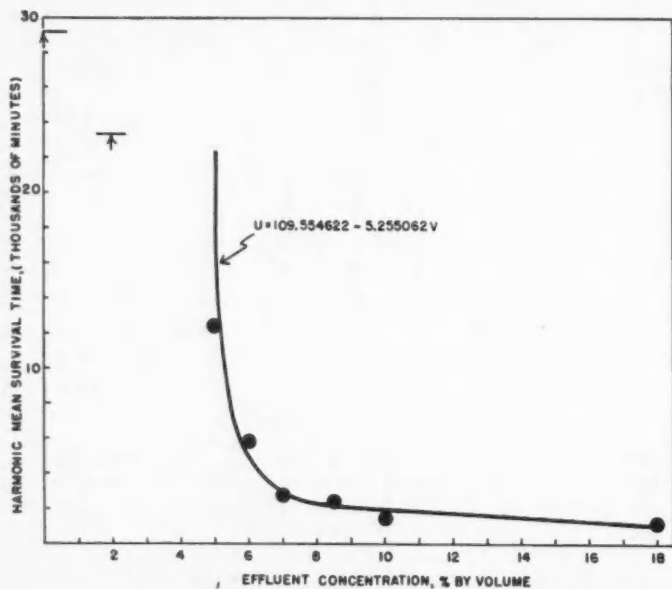


FIGURE 2. Relationship between the harmonic mean survival time in minutes for samples of sockeye salmon underyearlings and the concentrations of kraft mill effluent to which they were exposed. Arrows indicate times to which the control and the 2% effluent solutions were carried before termination of those series. The equation of the curve illustrating the relationship, $u = 109.554622 - 5.255062 v$, is derived in the text.

$$y - y_0 = \frac{K}{x - x_0}$$

where y = mean survival time, x = effluent concentration, and K , x_0 , y_0 are constants.

If $K \simeq (y_0 x_0)$, by rearrangement:

$$y = \frac{x}{\frac{1}{y_0}x - \frac{x_0}{y_0}}$$

Let $1/y_0 = \alpha$ and $-x_0/y_0 = \beta$; then:

$$y = \frac{x}{\alpha x + \beta}$$

and:

$$\frac{1}{y} = \alpha + \beta \frac{1}{x}$$

A special hyperbola is derived equivalent to the straight line:

$$u = \alpha + \beta v$$

where $u = 1/y$, the reciprocal of mean survival time; and $v = 1/x$, the reciprocal of effluent concentration.

A test for validity of this assumption was made by plotting the reciprocal mean survival times against reciprocals of the appropriate effluent concentrations. The resulting linearization (Fig. 3) indicates that a reasonably good fit is provided

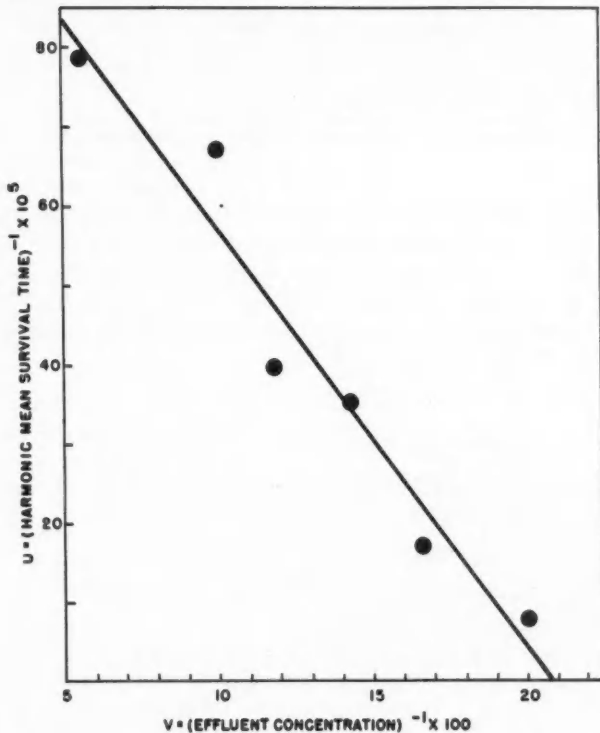


FIGURE 3. Regression of survival time on concentration of effluent to which sockeye salmon underyearlings were exposed.

by the special hyperbola. The asymptote $-\beta/a$ should provide an estimate of the concentration of effluent which is safe, in terms of the experimental fish, for all durations of exposure. Survival times at each effluent concentration, their harmonic means and the transformed data set out for analysis are listed in Table III.

TABLE III. Survival times in minutes for sockeye salmon underyearlings in a series of concentrations of kraft mill effluent. The initial sample size, n , at each concentration is 10. At each concentration, x , the proportion responding, r/n , at the times noted provides an estimate of the harmonic mean survival time, y , in minutes. The data are transformed for analysis: $u = y^{-1} \times 10^6$ and $v = x^{-1} \times 100$.

Mortality	Effluent concentration								
	r/n	0	2	5	6	7	8.5	10	18
0.10	a	b	5674(.11) ^c	4678	2125	...	954
0.20			2125
0.30			9276(.33)	4819	2370	...	1141
0.40			9910(.44)	1044	1142
0.50			11386(.55)	5219	1386	...
0.60			13492(.66)	2651	...	1695	1168
0.70			14828(.77)	6101	2114	1203
0.80			...	6826	2578	1743
0.90			...	9072	3099	...	2636	4079	...
1.00	24670(.77)	9424	3389	...	3084	4229	1883
y	—	—	12460	5867	2830	...	2518	1487	1272
u	—	—	8.026	17.044	35.431	...	39.715	67.231	78.646
v	—	—	20.000	16.667	14.286	...	11.765	10.000	5.556

^aNo mortality to termination of experiment at 29,176 minutes.

^bNo mortality to termination of experiment at 23,278 minutes.

^c $n = 9$. One fish injured while solutions were being changed was discarded.

It is required to fit the straight line $u = a + \beta v$ and to find a safe level of effluent concentration equivalent to v with $u = 0$, the reciprocal of v at this level being equivalent to the concentration of effluent below which there should be no mortality. With $u = 0$, v takes the value $-a/\beta$. Since $v = 1/x$, the value of x at $u = 0$ is the reciprocal, $-\beta/a$. An estimate of $-\beta/a$ is required with confidence limits for the true value of this quantity and estimates of the parameters a and β are represented by the letters a and b .

Setting down the normal equations

$$Nb + a \Sigma v = \Sigma u$$

$$vb + a \Sigma v^2 = \Sigma uv$$

$$\Sigma u = 245.993$$

$$\Sigma v = 78.274$$

$$\bar{u} = 40.999$$

$$\bar{v} = 13.045667$$

$$\Sigma u^2 = 13885.676075$$

$$\Sigma v^2 = 1151.163046$$

$$\Sigma uv = 2525.845165$$

$$N = 6$$

$$\Sigma (u - \bar{u})^2 = 3800.15007$$

$$\Sigma (u - \bar{u})(v - \bar{v}) = -683.29751$$

$$\Sigma (v - \bar{v})^2 = 130.026534$$

$$b = \left(\Sigma uv - \frac{(\Sigma u)(\Sigma v)}{N} \right) / \left(\Sigma v^2 - \frac{(\Sigma v)^2}{N} \right) = -5.255062$$

$$a = \bar{u} - b(\bar{v}) = 109.554622$$

$$-b/a = 0.0479675$$

The linear equation becomes

$$u = 109.554622 - 5.255062 v \text{ and the line is illustrated in Fig. 3.}$$

The residual sum of squares

$$\Sigma(u - \bar{u})^2 - \frac{[\Sigma(u - \bar{u})(v - \bar{v})]^2}{\Sigma(v - \bar{v})^2} = 209.37923$$

The error variance

$$s^2 = \frac{\text{s.s. residuals}}{N-2} = 52.344807$$

The elements of the inverse of the matrix of normal equations

$$C_{11} = \frac{1}{\Sigma(v - \bar{v})^2} = 0.007690738$$

$$C_{01} = -\bar{v} / \Sigma(v - \bar{v})^2 = -0.10033081$$

$$C_{00} = \frac{(\Sigma v^2)}{N} / \Sigma(v - \bar{v})^2 = 1.475549$$

Following Fieller's theorem (see Finney, 1952), if the value of $-\beta/a$ is λ , then $a\lambda + b$ is a linear function of the observations with mean zero and variance:

$$\begin{aligned} \text{Var}(a\lambda + b) &= \lambda^2 \text{Var}(a) + 2\lambda \text{Cov}(a, b) + \text{Var}(b) \\ &= \sigma^2(\lambda^2 C_{00} + 2\lambda C_{01} + C_{11}) \end{aligned}$$

where $\text{Var}(a) = \sigma^2 C_{00}$, $\text{Var}(b) = \sigma^2 C_{11}$, $\text{Cov}(a, b) = \sigma^2 C_{01}$.

Therefore, the expression:

$$\frac{a\lambda + b}{\sigma \sqrt{\lambda^2 C_{00} + 2\lambda C_{01} + C_{11}}}$$

is a standardized normal deviate and with σ the true value of s , replaced by an

estimate $s = \sqrt{\frac{\text{s.s. residuals}}{N-2}}$, has the t -distribution. Hence, with probability 0.95,

it lies in the interval:

$$-t_{.05} \leq \frac{a\lambda + b}{s \sqrt{\lambda^2 C_{00} + 2\lambda C_{01} + C_{11}}} \leq +t_{.05}$$

The two values of λ corresponding to the two equality signs provide 95% confidence limits for $-\beta/a$. They may be calculated from the rearranged form of these equalities. Hence:

$$(a\lambda + b)^2 = s^2 F_{.05}(\lambda^2 C_{00} + 2\lambda C_{01} + C_{11})$$

where $t^2_{.05}$ has been replaced by $F_{.05}$ with 1 and $N-2$ degrees of freedom. Gathering up terms in λ :

$$\begin{aligned} \lambda^2(a^2 - s^2 F_{.05} C_{00}) + 2\lambda(ab - s^2 F_{.05} C_{01}) + (b^2 - s^2 F_{.05} C_{11}) &= 0 \\ 11406.715459\lambda^2 - 1070.49962\lambda + 24.511861 &= 0 \\ \lambda = 0.03966 \text{ and } 0.05419 \end{aligned}$$

The concentration of effluent estimated to be safe in terms of the experimental evidence is calculated to be 4.8% effluent with limits of 4.0 and 5.4%.

INFLUENCE OF THE EFFLUENT ON OXYGEN REQUIREMENTS FOR RESPIRATION

Indications of periodic respiratory distress were observed throughout the testing period and consisted of a movement of the fish to the surface of the containers followed by "gaspings" ventilations in the period prior to exchange of the solutions. Rather few of these observations were obtained. Consequently, there is considerable spread in the distribution of points when the dissolved oxygen concentrations, at which respiratory distress was noted, are compared at various effluent concentrations (Fig. 4). However, a trend may be observed

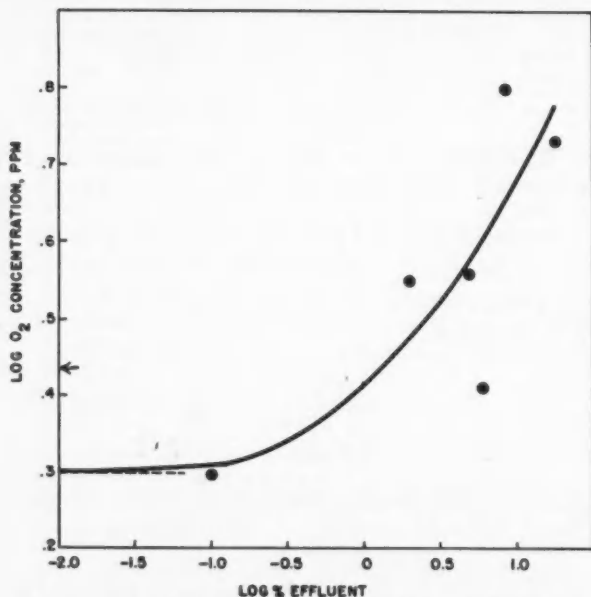


FIGURE 4. Relationship observed between level of effluent concentration and dissolved oxygen concentrations at which respiratory distress in test fish was noted. The dashed line refers to a "basal" requirement level adapted from Shepard's (1955) work (see the text), and the arrow points to an observation in the control solution. The entry at -1.0 log per cent effluent represents a 0.1 percent effluent solution which was discarded after 11,000 minutes.

in which indications of respiratory disturbance are manifested at progressively higher dissolved oxygen concentrations as the concentration of the effluent increases. Lacking better knowledge of the form of the curve, the relationship has been estimated by eye. The origin has been set at 2 ppm. dissolved oxygen, a level which Shepard (1955) demonstrated to be the incipient limiting level for a salmonid fish (*Salvelinus fontinalis*) when taken directly from air-saturated water. In the same study Shepard showed that young fish of this species could be acclimated to about 1.05 ppm. dissolved oxygen without significant losses. In the present case, fish initially were acclimated to air-saturation levels of dissolved oxygen. Although insufficient time was available in any 12-hour period for fish to acclimate fully to the diminishing oxygen concentrations, the limit of tolerance would probably be somewhat lower than 2 ppm. dissolved oxygen. However, to allow further estimation of dissolved oxygen requirements, the relationship in Fig. 4 has been used to provide an approximation of minimum dissolved oxygen requirements at various effluent concentrations (Table IV).

TABLE IV. Estimated concentrations of dissolved oxygen in various concentrations of kraft mill effluent at which hypoxial reactions were initiated.

Effluent, percent by volume	Dissolved oxygen, ppm.
0	2.00
2	2.99
4	3.59
6	4.03
8	4.52
10	4.82
12	5.13
14	5.48
16	5.73
18	6.00

DISCUSSION AND CONCLUSIONS

Kraft mills discharge large volumes of effluent into waters inhabited at various intervals by migratory stages of Pacific salmon. Since the effluent which is discharged from the mill requires further dilution and oxidation to render it innocuous to fishes, consideration of the toxicity of the effluent involves the volume of the effluent, the volume of receiving water into which it flows and the rate of replacement of their combined volumes.

A number of studies have been conducted on the toxicity of the components of kraft effluent to various fishes and fish-food organisms (e.g. Anon., 1952a, Haydu *et al.*, 1953). The State of California Water Pollution Control Board has summarized information in this regard (Anon., 1952b); of the many components, the resin and fatty acids, their salts, and the sulphur containing compounds such as sodium sulphide, hydrogen sulphide, methyl mercaptan, sodium thiosulphate and sodium hydrogen sulphide show the greatest toxic effects. Sulphides and mercaptans are said to be readily destroyed on contact with the dissolved oxygen present in receiving water (Gehm, 1953) and are seldom detectable, except at the point of discharge.

If the downstream migrant may be assumed to be the more vulnerable stage in the anadromous cycle of the Pacific salmon, conclusions reached from examination of this stage of development may suggest the level of effluent concentration to which these fishes can be regarded as tolerant.

Gehm (*loc. cit.*) concludes that toxic conditions will not be approached when the dilution ratio of mill waste to receiving water is 1:20 or greater. Results of the present tests indicate that the concentration limit might be set slightly lower for freedom from toxic effects *per se* in this specific instance; a 5% effluent concentration resulted experimentally in 50% mortality after slightly more than a one-week exposure. The concentration of effluent below which mortality is calculated not to occur from the present tests is 4.8% effluent, or a ratio of about 1:21 with the receiving water.

It is well known that the lethality of many toxic substances is increased by concomitant low dissolved oxygen conditions. Studies of the Water Pollution Research Laboratory (Anon., 1952a, 1953, 1954), for example, indicate that the toxic effects of ammonium ion and of cyanide may be increased by a reduction of dissolved oxygen concentration within the range of respiratory tolerance. In the present study the lowered oxygen levels likely influenced the measured toxicity response to some extent. Although no deaths in effluent solutions could be attributed directly to hypoxia, the stress placed upon test fish would be increased by low-grade hypoxial conditions present in the test solutions for approximately the latter quarter of each 12-hour period throughout the course of the experiment. The added metabolic load imposed on the test fish could increase their rate of loss of tolerance to the effluent solutions.

If dissolved oxygen values had been held near saturation level in all solutions, the tests would have been less representative in view of the fact that dilution of the effluent initially may provide an area of lowered oxygen concentration by virtue of its low oxygen content and secondarily, the diluted effluent may provide another region of lowered oxygen concentration by virtue of its oxygen demand. The interaction of effluent toxicity and lowered oxygen availability may be regarded, therefore, as a better criterion than toxicity alone for the assessment of responses of young salmon to kraft effluent. Results of the assays are considered to be reasonable approximations to those conditions.

Waldichuk (*loc. cit.*) has calculated the oxygen consumption of the effluent at the Alberni outfall, movement of water masses in the adjacent estuary of the Somass River, and the oxygen replacement to that zone by various levels of Somass River discharge. A comparison of oxygen supplies available after effluent oxidation, as calculated by Waldichuk, with estimated respiratory requirements herein estimated (see Fig. 4) for migrating salmonids, shows that oxygen requirements for respiration are of first importance. In this particular example, dissolved oxygen levels define the safe level of effluent concentration at about 2.5% effluent by volume, or a ratio of effluent to receiving water of about 1:40 (Fig. 5).

It might be assumed that resistance to water-borne toxic substances would increase with age and size of fishes. This may not be generally true. Williams *et al.* (1953) provide evidence which indicates that resistance to *sulphite* waste

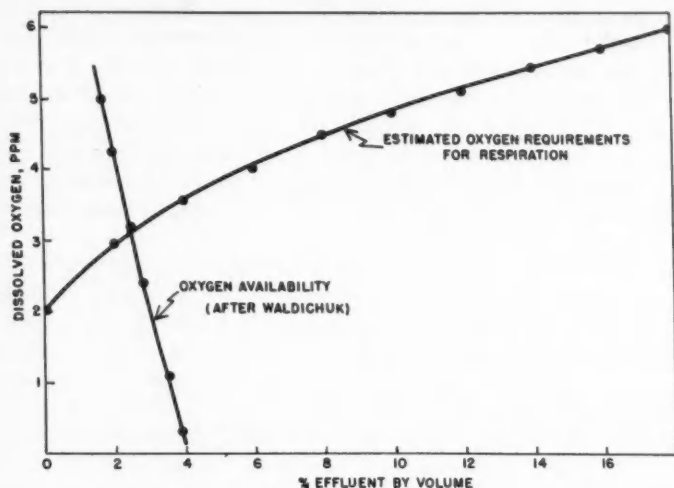


FIGURE 5. Comparison of calculated net oxygen availability after effluent oxidation with respiratory requirements of sockeye salmon underyearlings at various concentrations of kraft mill effluent. The point of intersection of the curves, equivalent to a concentration of 2.5% effluent in the receiving water, provides an estimate of the concentration of effluent at which oxygen availability becomes a limiting factor for fishes in terms of the test conditions (see the text).

liquor decreases with development in three species of Pacific salmon within the first year. Pink (*O. gorbuscha*), coho and spring salmon at various ages up to 412 days described a loss of tolerance quite consistent with advancing age. The samples used in the present study were approximately 6 months old. Although data are not available on the possible variation in tolerance with age of the present samples to sulphate effluent, conformity in general with sulphite waste liquor findings would place the young sockeye salmon used here about midway within the range of changing resistance with age. A comparison with their results implies that pink, chum (*O. keta*), spring and coho migrant fry would be more resistant, and sockeye and coho migrant yearlings less resistant than the present results would indicate. Further studies are necessary to examine these possibilities.

SUMMARY

Experimental evidence is presented concerning the resistance of sockeye salmon (*Oncorhynchus nerka*) underyearlings to kraft mill effluent. This study was undertaken to provide information on "safe" levels of effluent concentration resulting from the discharge of effluent, from the proposed expanded production of a sulphate mill, into an area including the Somass River estuary at the head of Alberni Inlet, B.C. Three species of Pacific salmon, including the sockeye, move through this region as both spawning and seaward migrants.

Samples of the test fish were exposed to concentrations of 2, 5, 6, 7, 8.5, 10 and 18% effluent by volume. Solutions were made up with refrigerated 24-hour composite effluent and sea-water adjusted to a salinity of 20‰. Times to death in the various concentrations were noted and mean reciprocal survival times were calculated for each effluent solution, the stimulus-response distribution resembling a rectangular hyperbola. Experimental evidence indicates that under the test conditions, the effluent concentration below which mortality would not occur from toxic effects *per se* is 4.8 (4.797) per cent effluent with limits of 4.0 (3.966) and 5.4 (5.419) per cent.

Hypoxial behaviour of test fish under diminishing oxygen levels in the test solutions showed an increased oxygen requirement for respiration with increased effluent concentration. Although the nature of the relationship describing the increased demand is not defined with precision, results of this study indicate that attention to respiratory requirements of fishes exposed to effluent is of primary importance in defining the permissible concentration of effluent at any mill site. The oxygen demand of the proposed Alberni effluent, net oxygen availability after effluent oxidation and dependence of respiratory requirements on the level of effluent concentration required that the former figure of 4.8% be reduced to 2.5% effluent by volume for fish safety.

ACKNOWLEDGMENTS

The assays conducted in this study represent one aspect of a programme which was carried out to advise MacMillan and Bloedel Ltd., operators of the Alberni and Harmac pulp mills, on methods of circumventing pollutional problems envisaged by the operators. Various portions of the programme were carried out by the B.C. Research Council, Division of Applied Biology, and Dr. M. Waldichuk of the Biological Station, Nanaimo, with Dr. J. P. Tully of the Pacific Oceanographic Group acting in an advisory capacity.

It is a pleasure to acknowledge the co-operative effort by which this programme was carried out, particularly with regard to members of MacMillan and Bloedel Ltd., who offered information and supplies of effluent in the present study.

The writers are indebted to Dr. D. DeLury, Ontario Research Foundation, for his assistance in the selection of the statistical procedures.

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APPENDIX

Empirical relationships have been estimated for the interaction of effluent toxicity and oxygen requirements for respiration. The general conclusions drawn require some further interpretation, however, before they may be applied under the particular circumstances in Alberni Inlet. Coincident high effluent levels and low oxygen saturation values occur only in the immediate vicinity of the mill outfall (Waldichuk, 1954b), and then only in the very shallow surface-water layer. It is estimated that under present conditions, interference with seaward-migrating salmon might only be anticipated from the effluent "slug" in the immediate vicinity of the outfall if such migrants were to remain in this restricted area for a period in excess of about two days. Such behaviour is considered to be improbable.

As the effluent becomes diluted with sea-water and Somass River water at the head of the inlet, oxidation of effluent components will occur. A 5-day B.O.D. for the diluted effluent is approximately 150 ppm. (Waldichuk, 1954b). Under usual conditions the rate of transport of water seaward from the head of the inlet (Tully, 1949; Waldichuk, 1954b) infers that any drop in oxygen concentration ("sag") which may occur will take place in the upper waters of the inlet in an area approximately two to three miles seaward from the mill outfall. Although a very slight oxygen sag has been reported from this area under existing circumstances (Waldichuk, personal communication), the almost negligible oxygen depletion and effluent levels in the region are at present considered to be of no biological concern. Increased mill production and concomitant increases in effluent volume and oxygen demand will increase the area and magnitude of oxygen sag as well as the concentration of effluent in the upper waters in the head of the inlet. Present results suggest that the latter should not exceed 2.5% effluent in an area large enough to form a potential block to seaward migration of young salmon. It is estimated that interference with migration would begin were the 2.5% effluent contour to extend through the area of oxygen sag with oxygen depletion in the latter area resulting in a final oxygen concentration of 3 to 3.5 ppm. before recovery.



